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*A Journal Dealing with the Transmission and Processing of Information
as well as with Control Processes in Both Organisms and Automata*

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Die Begriffe Nachrichtenübertragung, Nachrichtenverarbeitung, Steuerung und Regelung sind im Bereich der Technik und Physik entstanden. Sie werden aber heute nicht nur in der Nachrichtentechnik und Automatisierungstechnik angewendet, sondern auch im biologischen Bereich. Denkverfahren, wissenschaftliche Erkenntnisse und mathematische Methoden aus diesen physikalisch-technischen Gebieten lassen sich vielfach auf Vorgänge im Organismus übertragen. Ihre Anwendung auf Probleme der Rezeptor- und Nervenphysiologie hat zu neuen Erkenntnissen über die im Organismus verwirklichten nachrichtentechnischen Prinzipien geführt. Umgekehrt zeigt sich ein wachsendes Interesse der Technik, Physik und Ingenieurwissenschaften an den Vorgängen der Nachrichtenübertragung, -verarbeitung, Steuerung und Regelung im lebenden Organismus. Die bessere Erkenntnis solcher Vorgänge kann wichtige Hinweise auch über technische Möglichkeiten geben, wie z. B. bei der Frage nach dem Wesen des Lernens.

Die Zeitschrift für Kybernetik soll diesen Erfahrungsaustausch fördern, indem sie besonders folgende Gebiete pflegen will: Informations- und Systemtheorie, Steuerungs- und Regelungstheorie, wissenschaftliche Grundlagen und grundsätzliche Verfahren der Nachrichtenverarbeitung, experimentelle Ergebnisse der Rezeptorphysiologie und der Nervenphysiologie im Hinblick auf die Nachrichtenverarbeitung und -übertragung; Steuerung und Regelung im Organismus; Verhalten von Organismen und Gruppen von Organismen bei Aufgaben der Nachrichtenübertragung und -verarbeitung; Nachrichtenverarbeitung durch den Menschen; Modelle für die Nachrichtenübertragung und -verarbeitung im Organismus.

The concepts of transmission of information, processing of information and automatic control engineering originated within technology and physics. Today, however, these concepts have also found application in the biological sciences. The logical procedures, the methods of experimental and theoretical approaches and the mathematical techniques that are applicable to the physical sciences can often be successfully transferred to the realm of the life sciences. By applying those techniques to sensory and neurophysiological problems new insight has been gained into the principles by means of which organisms handle information. Conversely, physicists and engineers have shown increasing concern for the mechanisms that organisms have evolved in the areas of communication and control. The understanding of these mechanisms may have significant technological consequences as, for instance, in relation to the nature of learning process.

»Kybernetik« would like to cultivate experimental and theoretical findings in the following fields: Information theory; theory of automata; theory of control systems; mathematical foundations of communication theory; sensory processes and micro- and macrophysiology of the central-nervous-system in relation to information handling; information handling by organisms (incl. man) and task-oriented groups; mathematical models for communication and control processes in organisms.

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Studies with Artificial Neurons, I: Properties and Functions of an Artificial Neuron

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With 21 Figures in the Text

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Summary. 1. A brief outline of the evolution of neuron modeling is given and an argument is presented for studying neural behavior by "black-box" logical equivalence.

2. An electronic circuit incorporating many of the digital and analog properties of neurons is described. Having such properties as variable threshold, summation, all-or-none output, absolute and relative refractoriness, and inhibition, it exhibits a considerable amount of functional equivalence to biological structures.

3. Properties of the model are described in detail and its advance to biological neuron measurements are shown. Such behavior as time-intensity trade, repetitive firing and temporal summation are readily achieved and are shown to approximate *in vivo* behavior.

4. The model is sufficiently flexible so that with simple parameter changes and external circuit configurations, a wide variety of neurological phenomena can be exhibited and studied closely. By adding stimulus-derived inhibition, for example, accommodation and adaptation are obtained.

5. Experiments with the model have suggested new relationships which nervous structures may exhibit. A linear dependence of burst pulse number on accommodation time constant, and a summation-division phenomenon are examples of such findings.

6. Models of this sort have utility not only for studying single unit properties but also for investigating group interactions. Such studies may be relevant to elucidation of neural network behavior.

Introduction

In attempting to understand nervous systems, one may ask questions on at least four different levels. At the subcellular level are studies such as those of transport mechanisms and membrane properties. Secondly, single cells may be studied for their input-output functions, the stimulus-response relationships. At another level, groups of cells are investigated in terms of their interactive behavior; this ranges from simple systems such as reflex arcs to neural pools and organized mass actions. Finally, there are the psychophysical investigations of the entire organism viewed as a "black-box".

The research reported here takes for its locus the cellular input-output functions level, seeking to explore the "logical" properties of the single neuron by the use of analog models. It is also directed in part to the third of the foregoing categories, i.e., to an investigation of the interactions of small numbers of these units. It seeks to explore some of the information processes encoded in neural activity.

In the past, biological systems have been regarded in such terms as metabolism, electrical activity, reproduction, and movement. It is increasingly apparent that in addition, the processing and flow of information is a relevant property. This is especially true for nervous systems. The present work is based on the

view that the essential role of neural structure is to manipulate information; neural events represent the language of this process. Such an approach is not concerned with detailed electrical, chemical or ionic events within a cell, but only with their ultimate operational effects. Neural functions can (in principle) as readily be specified with electronic circuits or mathematical symbols as with ion-membrane mechanisms. It is essential only to preserve the fundamental logical operations. Thus, chemical, electronic and mathematical systems may all be expressions of identical functions and may be used interchangeably as statements of the same mechanism.

Modeling of neural properties is not new. Sixty years ago HERMANN (1899) considered nervous activity in terms of electrical cable behavior. LILLIE (1936) described a chemical model of axon conduction which was subsequently greatly elaborated by others. A large number of mathematical models have appeared in the literature, of which those of McCulloch & Pitts (1943), Hodgkin & Huxley (1952b), Minsky (1953), Kleene (1956) and von Neumann (1956) are representative. Electronic analogs of neural properties have been described by Burns (1955), Harmon (1959), Crane (1960) and Küpfmüller & Jenik (1961). Computer simulation studies such as those by Rochester (1956), Willis (1959) and Farley & Clark (1960) et al. have been directed to investigating neural network behavior.

Electronic analogs of neurons provide a flexible means for exploring the logics of the nervous system. It is relatively easy to incorporate a large number of parameters representative of the biological cell. The model may then literally be used as an analog computer to examine functions that may be exceedingly difficult if not impossible to predict or to fully analyze. The studies described in this paper take for their premise that such simulation can have utility and that continued exploration with such models can lead to a better comprehension of neural events.

There has been a sharp increase in neural modeling activity during the last few years, and it is important to point out that two distinct philosophies are involved. One school, of which the present work is representative, seeks to make its "neurons" simulate biological functions as closely as possible. Input-output relationships are made to be consistent with what is known of the biological parameters. The intent is to study the probable information-processing functions of neurons and in so doing to elucidate further the operations of the biological system.

Among the second group of modelers (by far the most populous) the idea is to explore the large-scale behavior of many quasi-neuron elements arranged in randomly connected nets. Inasmuch as the properties of these elements are greatly simplified abstractions of known neural functions, and the network connectivity bears no necessary resemblance to biological structure, it seems unlikely that results bearing real physiological significance will emerge.

There is reason to confine our present studies to peripheral mechanisms. Little enough is known of function at the transducer levels and the early relay stages; firm knowledge of cortical events is even less detailed and secure. The peripheral structures are simpler, are better known anatomically and physiologically, and are more accessible to experimentation than are the central structures. Furthermore, it would appear useful to understand the mechanisms of the retina and the optic nerve signal encodings, for example, before attempting to comprehend more central events. Certain recent studies (KUFFLER, 1953; HUBEL & WIESEL, 1959; LETTVIN, MATURANA, McCULLOCH & PITTS, 1959) illustrate the utility of this view.

The Model

Most of the models proposed to date have incorporated the classical axonal properties of temporal summation, variable threshold, inhibition, refractory recovery and all-or-none output. It has become apparent, however, that the properties of the entire neuron must be simulated. This means that adequate provision must also be made for the graded dendritic functions having longer time constants and decremental conduction.

Although a considerable amount of important activity is assignable to these continuous-variable input functions (as opposed to axonal discrete-variable behavior), there is no compelling reason to believe that axon action potentials do not represent the principal *language* of the peripheral nervous system. We recognize BULLOCK's (1959) observation that axon spikes are not seen in some neural structures and his conclusion that they may be incidental and superfluous to function. Nevertheless, if we take as a functional neural unit the system from dendritic ramifications to axonal termini, it is clear that however diffuse, graded, and smeared in time the input signals may be, the functional output is unique, standardized (to a first-order approximation) and is crisply defined. All-or-none activity assuredly accounts for more than long-distance transmission; for example, the concomitant refractory phenomena clearly play an important role in modifying signals.

Thus, it is useful to consider that there are two kinds of information processing present. In one, the intracellular continuous-variable processes are significant. In the other, discrete but variable signals between cells operate to transmit and to modify information. Both are essential to a complete description of neural events.

The model¹ we use is electronic, being a circuit of five transistors and associated resistors, capacitors and

diodes. An earlier version was described (HARMON 1959) in which the functions were less accurate and flexible than they are presently. A detailed circuit analysis of that version appears in HARMON & WOLF (1959). The present version, which retains the basic structure of the earlier one, is shown in Fig. 1.

Five excitatory inputs are integrated by their associated 150 K Ω resistors and the 0.02 μ F capacitor on the base of the first transistor T_1 . Depending on how the input (dendritic) leads are connected to various (axon or receptor) sources, the integrating time constant can be varied from 0.46 to 1.2 msec. Threshold is determined by the relationship between the potential on the base of T_1 (corresponding to the time course of input signals) and the potential on the emitter of T_1 (depending upon the recent firing history of the unit). T_1 and T_2 together form a monostable multivibrator whose function is to produce a single pulse if threshold is exceeded. T_3 and T_4 form an amplifier and low impedance output source such that as many as 100 other units may be driven directly, if desired. The function of T_5 is to invert an otherwise excitatory signal. The inverted signal is summed with the five excitatory inputs to produce inhibition.

The refractory function is obtained from the time constant associated with T_1 and T_2 , whose pulse emitting activity may be inhibited by a graded change in their virtual threshold. The circuit provides an absolute refractory period which is approximately 1.0 msec long (the output pulse duration) and which is immediately followed by a decaying exponential recovery to resting threshold having a time constant of 2.7 msec. As will be shown, this and the input time constant may be readily modified over a wide range to simulate a variety of neural mechanisms.

The neuromime has a transmission delay that varies from 0.1 to 1.0 msec depending on input connections and on firing frequency. Because of the nature of the active electronic components, the unit permits unidirectional propagation only, i.e., no antidromic stimulation is possible.

Inhibition is a continuous (graded) and essentially linear function of the potential applied to the inhibition input. Two quite different kinds of inhibition have been described for biological preparations. In one, an inhibitory impulse increases resting membrane potential, thereby increasing the threshold for excitatory impulses (BROCK, COOMBS, & ECCLES 1952). In the other, inhibitory impulses diminish any local polarization or depolarization which may be present, tending to restore resting potential (FATT & KATZ 1953). Thus in the first case inhibition may be viewed as an active potentiating process while in the second it is effectively a passive attenuation. The former process is subtractive, the latter multiplicative. In the present design of the neuromime the first process is modeled.

Any number of excitatory or inhibitory inputs are possible, of course, since multiple inputs can be converged into any combination of the five excitatory and one inhibitory leads. Each input can have additional resistive networks appended to obtain decremental conduction, and auxiliary capacitors may be added to obtain long time constant, graded dendritic behavior. This leads to latencies which act in addition to the simple internal delay mentioned above. Diodes

¹ In a proposal for a systematic nomenclature of devices which simulate biological functions, VAN BERGELJK (1960) suggested the term *neuromime* for neuron models. We adopt this designation in subsequent references to the artificial neuron.

lation between units can be arranged, if required, minimize interference or loading between multiple living units.

There appears to be some evidence that the transmission properties of synapses in the CNS vary with the intensity of the stimulus (ECCLES & McINTYRE, 1953). Although we have developed models for obtaining variable synaptic impedance, they are not being employed in present experiments and will not be described here. We do not introduce them for two reasons: first, the evidence for variable synaptic behavior is incomplete and controversial; second, peripheral (e.g. retinal) structure may be assumed to be relatively invariant, and there seems little necessity at present to invoke synaptic changes as functions of experience at this level.

The primitive functions of the neuromime are summarized in Table 1.

Table 1

Resting threshold	—1.5 V for steady, transducer-like input (rheobase) —3.0 V for typical single spike input
Temporal summation	Time constant: 0.46 to 1.2 msec, depending on input configuration
Delay	0.1 to 1.0 msec, depending on firing frequency and input configuration
Spike output	0.8 to 1.2 msec pulse of —10 V amplitude
Refractoriness	Absolute: ≈ 1.0 msec Relative: 2.7 msec time constant
Firing frequency	0—600 pulses per second
Inhibition	Graded subtraction from excitation
Power consumption	81 mW

The magnitudes of the voltages employed in the model do not correspond to biological levels. This is not important, however, because the voltage ratios are similar to the natural ratios. For example, the 7:1 ratio of spike amplitude to rheobase in the model approximates the 7:1 safety-factor described for biological preparations (HODGKIN 1937, 1948). The temporal relationships closely approximate those in natural neurons. While it may be argued that a rectangular output pulse of 1 msec duration having no subnormal or supernormal phases is too gross a representation of the spike potential, our feeling is that the discrepancies introduce negligible differences in over-all functional (logical) behavior. Should the discrepancies turn out to be significant, it would be relatively easy, as will be shown, to modify the model to provide differentiated output or post-output polarizations.

Several natural neural properties are not incorporated in the model. For one, conduction velocity along input or output leads can be made neither slow nor variable. This means that there is no "event" delay other than two simple types of internal latencies which will be described. However, the neuromime can also be considered as a section of myelinated axon rather than as a complete cell. If a number of units are connected serially, then conduction is saltatory; each unit represents a node, while the connections between them represent rapidly conducting internodes. In this way, various transmission delays may be achieved. A second omission is that, with the exception of the very rapid dynamic flip-flop action

of the pulse generator, excitation does not grow after removal of a stimulus. Therefore, the model is, with that exception, passive. A third omission is the possibility of making a given input lead excitatory at one time and inhibitory at another; thus, there is no equivalent here to the presumed functional change of presynaptic fibers dependent on post-synaptic membrane potential (FATT, 1954; GRUNDFEST, 1959). We shall show, however, that despite these deficiencies, the model is sufficiently complete to simulate a number of biological phenomena.

The neuromime has three primitive input-output properties. They are one-to-one, where a single spike elicits a single spike; one-to-many, where a step function or steady potential results in a train of output pulses (as in peripheral transducers); and many-to-one,

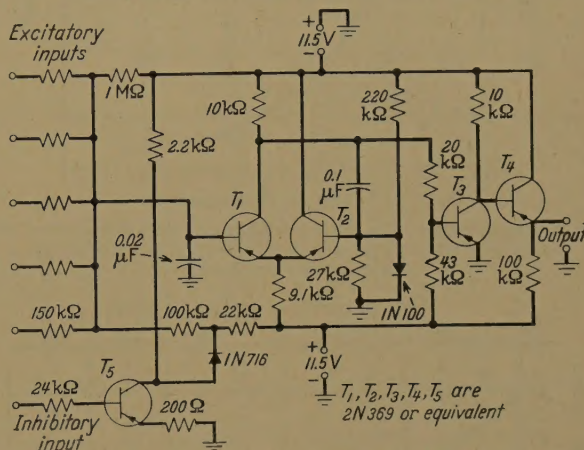


Fig. 1. Circuit diagram of artificial neuron

in which spatial or temporal summation occurs. (We ignore for the present a fourth possibility, namely those outputs which result from no input, as in spontaneous firing.) These properties which include such time-varying characteristics as excitation, threshold and inhibition are sufficient to produce a vast number of logical functions. These include "and", "or", "not", "if-and-only-if", addition, subtraction and division, as well as more complex operations such as filtering, differentiation, and counting.

Some properties of the model

Some of the typical characteristics of the neuromime are illustrated in this section. These are the primitive properties of the circuit shown in Fig. 1 and do not include functions such as accommodation and adaptation. It will be shown later how these more complex operations can be built up from the primitive ones.

Due to component tolerances, there is some spread (on the order of 10%) in performance between units. The following results show the measured responses of an average unit.

Time-intensity trade. For a given pulse input to a biological neuron, there is a minimum time required for a given intensity to elicit a response (ARVANITAKI, 1938). The behavior of the model closely approximates ARVANITAKI's strength-duration results as is shown in Fig. 2. We see, for example, that a 2.7 V stimulus must be at least 1.0 msec long to cause firing, while one having an amplitude of 1.68 V must last for a

minimum of 3.0 msec. The horizontal asymptote of this curve, roughly 1.5 V, represents the rheobase. The shape of the curve is a direct consequence of the exponential input characteristic. The instantaneous potential $E(t)$ available at the summing input is

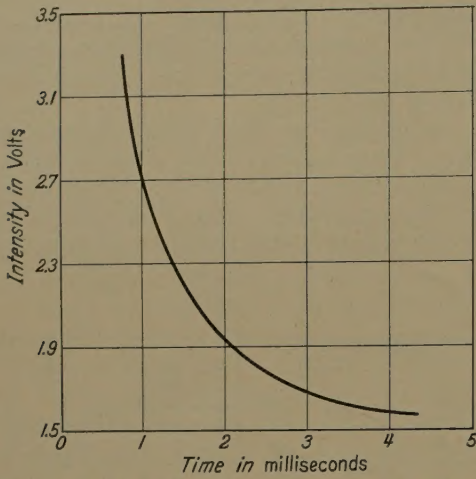
$$E(t) = E_{\max} (1 - e^{-t/k}) \tag{1}$$


Fig. 2. Time-intensity trade for threshold firing. Since firing occurs just at the termination of the stimulus, the curve also represents the strength-latency relationship

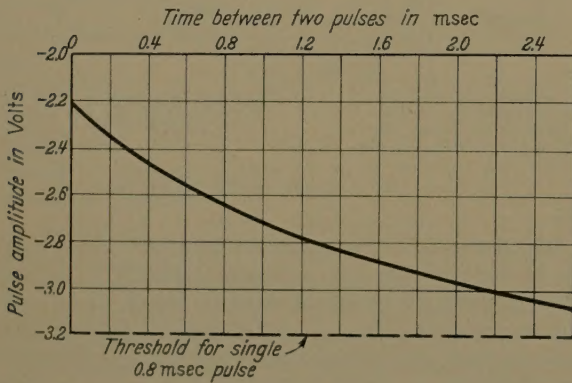


Fig. 3. Temporal summation for two 0.8 msec pulses of equal amplitude. Indicated times are from the termination of the first pulse to the onset of the second. Amplitudes are those required to just elicit firing

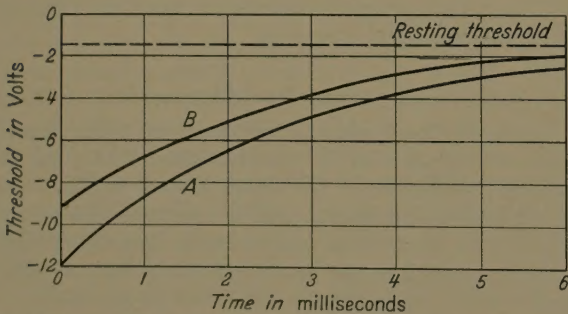


Fig. 4. Exponential refractory recovery of artificial neuron. This relatively refractory phase is preceded by the absolutely refractory time (output pulse duration) which terminated at $t=0$. Curve A results from the use of one input lead; the recovery in B is due to more effective excitation derived from three input leads used in parallel

where $E_{\max}$ is the amplitude of the pulse stimulus, and k is the time constant of the input integrator (1.2 msec). Each point on the curve represents the condition $E(t) = E_{\text{rheobase}} = \text{const}$. Thus as the intensity ($E_{\max}$) is increased, t must decrease. This is the equivalent of the familiar relationship

$$I_{\text{rheobase}} = I_{\text{stimulus}} (1 - e^{-t/k}).$$

Latency. Latency in the model is conventional defined as the delay of impulse initiation in response to a stimulus of long duration. Since there is no internal regenerative process contributing significantly to firing delay after the removal of a stimulus, latency is principally due to the gradual build-up of potential in the input integrator. Firing occurs as soon as the threshold is exceeded. Hence, the strength-duration curve of Fig. 2 is also a strength-latency curve. The results are similar to those described for motoneurons (FRANK & FUORTES, 1956). The curve is asymptotic to about 0.5 msec which represents the minimum firing delay in the pulse generating circuit.

Temporal summation. The time-intensity relationships required for the sum of two subthreshold pulses to elicit firing are given in Fig. 3. Each point along the abscissa indicates the elapsed time between the end of the first pulse and the onset of the second. Points along the ordinate indicate the minimum pulse amplitude (equal for both pulses) required to just elicit a response. This behavior too, is the straightforward result of the input integration characteristic and it is similar to the synaptic summation described by ECCLES (1946).

It is seen that time and intensity in the model can be traded over a range of about one volt, which amounts to approximately 10% of the amplitude of a typical output pulse. Summation can be achieved over a time ranging from 0 (temporal coincidence) to about 3 msec, for which time the required amplitude of the first pulse is sufficient to exceed resting threshold. Longer time constants of facilitation may be readily obtained by introducing additional integrating elements (R and C) at the input.

Refractory recovery. Typical recovery after firing is shown in curve A of Fig. 4. This is similar to the recovery of biological neurons after inactivation (ECCLES, LANGER & GASSER, 1937; HODGKIN & HUXLEY, 1952a). The neuromime is absolutely refractory for approximately 1 msec, the duration of the output pulse; the relative refractory state, beginning at $t=0$ in this illustration, starts at the cessation of the pulse (ADRIAN, 1921). This exponential recovery toward the resting threshold has a time constant of 2.7 msec. Recovery is effectively complete in about 20 msec since a rheobasic stimulus applied at this time will once again elicit firing.

This curve results from the use of one input lead. In B, three leads, used in parallel, increase the effect of a stimulus. Thus, the refractory level will appear reduced while its time constant remains unchanged.

Output pulse. The all-or-none rectangular output pulse has relatively constant amplitude; its width, however, changes somewhat as a function of firing frequency. This is shown in Fig. 5. This behavior is a consequence of several interacting circuit parameters and was not deliberately designed. It has a slight effect on temporal integration (reducing its efficiency with increasing frequency up to 500 pps but probably negligibly alters the neuromime's behavior. Diminution of spike amplitude with increasing frequency has been described by RENSCHAW (1942), KUFFLER (1953) and others. If the subsequent effectiveness of a spike is determined by its energy (time amplitude integral), then reduction of pulse-width with

¹ pps = pulses per second.

creasing frequency can have the same end result as amplitude change. Such duration-amplitude interchangeability is known to hold, for example, in the documented time-intensity trade relationships.

Delay. This term refers to the time between the beginning of a driving pulse and the onset of an output pulse during continuous pulse stimulation. It is not delay in the usual sense. Latency, generally measured for single pulse or for step-function stimulation, does not involve post-firing refractory phenomena. Delay in the model is a function both of excitatory processes (input integration) and of refractory recovery. Typical behavior is shown in Fig. 6.

Curve *A* depicts the delay as firing frequency is increased and applied to a single input lead ($k = 1.2$ msec). As a driving frequency of about 250 pps is reached, the driven unit "drops out", and its firing frequency decreases discontinuously to a lower value. This phenomenon is due to some interesting relationships between input and refractory time constants which will be discussed later.

Curve *B* illustrates the behavior for all five inputs strapped together making $k = 0.46$ msec. Here the driven unit "follows" the input pulses up to its maximum rate. In addition, the amount and variability of the firing delay is reduced. In both cases *A* and *B* delay increases with frequency because progressively less refractory recovery is encountered at the onset of each driving pulse.

Repetitive firing. The generation of a continuous train of impulses for a constant stimulus is readily achieved by the model. Repetitive firing in neurons has been attributed to interaction of a constant stimulus with refractory recovery (ADRIAN, 1930; HODGKIN, 1936). In another view (HODGKIN, 1948), it is a function of a periodic internal excitation process which must be repeatedly "charged-up" by the constant applied stimulus. The repetitive firing characteristic of the present model combines both viewpoints: the input integrator is partially discharged with each firing; this works in combination with the exponential refractory characteristic to determine the firing rate, although the latter parameter is the dominant one.

Fig. 7 shows firing frequency as a function of steady input voltage for two different input configurations. Curve *A* results from the strapping together of three of the five excitatory input leads to obtain an integration time constant of 0.66 msec. Curve *B* is obtained by using a single input lead where $k = 1.2$ msec.

When driven by a steady input, both configurations produce reliable firing frequencies over a range of about 50–600 pps. When a pulse source is used (such as another unit) the response frequency has no minimum.

If an extremely low firing frequency for small, steady excitation levels is required, an external feedback loop from output to inhibitory input readily produces it. Fig. 8 shows the arrangement.

Each output pulse is integrated with a time constant τ which is determined by the choice of R and C , and is applied to the inhibition input. Consequently, a decaying exponential voltage appears at the inhibition input after termination of the output pulse.

Diode isolation¹ is required to prevent C from discharging into the output line. The effect of this circuit is simply to prolong the relative refractory time.

For $R = 0.5$ M Ω and $C = 1.0$ μ F, stable repetitive firing continues smoothly down to 5 pps. This is shown as dotted extensions of the curves of Fig. 7.

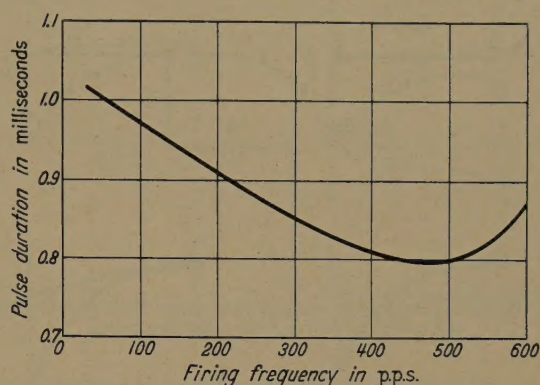


Fig. 5. Variation of output pulse width (duration) with firing frequency. Pulse amplitude remains constant

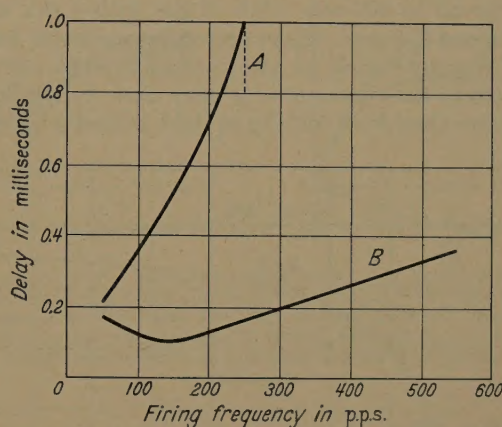


Fig. 6. Total delay from the beginning of a stimulus pulse in a repetitive train to the firing of a typical unit. Characteristic *A* holds for a long time constant input integration; *B* results from a shorter time constant and concomitant stronger excitation. See text for details

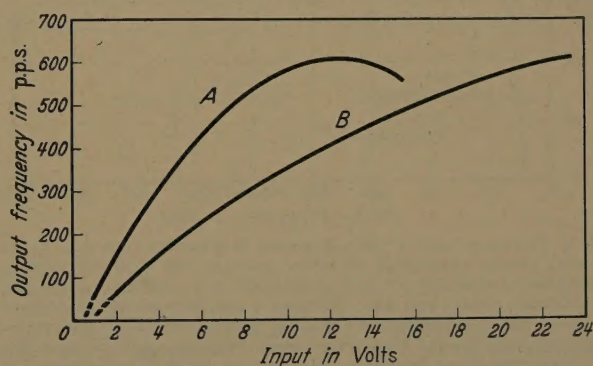


Fig. 7. Repetitive firing frequency as a function of stimulus level for two different input configurations. *A* — Three input leads used in parallel. *B* — One input lead. Stable firing down to 50 pps is obtained. This lower limit can be extended by a simple circuit addition

Repetitive firing frequency in biological preparations has been shown to be approximately logarithmic.

¹ The only elements besides the basic model circuit used in any of the experiments described are resistors, capacitors, and diodes. The first two components are generally employed to provide additional integrative mechanisms and decremental conduction. Diodes may be considered as rough analogs of some synaptic mechanisms and are introduced only where their logical function does no violence to neurophysiological evidence.

mically related to the stimulus intensity on receptors (HARTLINE, 1938; GRANIT, 1947; KATZ, 1950); in other studies firing frequency has been found to be linearly dependent on generator potential up to 60 pps (FUORTES, 1959) and up to 300 pps (KATZ, 1950). The frequency-excitation curves of the neuromime (Fig. 7)

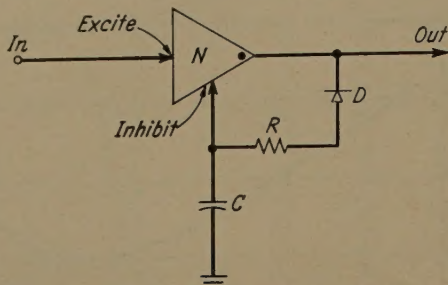


Fig. 8. Circuit arrangement to extend low-frequency limit of stable firing. Self-inhibition prolongs the refractory period

are quasi-logarithmic. The low-frequency sections are essentially linear; characteristic *A* lies within 3% of linearity up to 300 pps, while *B* lies within this limit up to about 250 pps. When driven by nonlinear transducer elements such as photo-resistors, the over-all response of the neuromime is very close to log-linear over more than four decades of light intensity change.

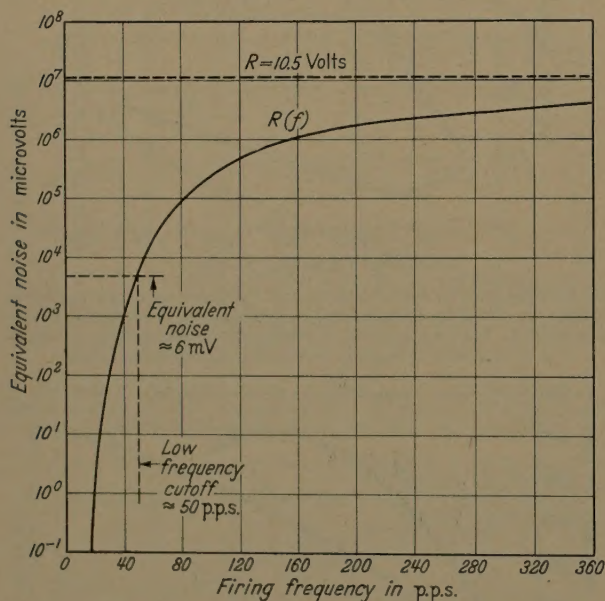


Fig. 9. The lower limit of firing frequency is determined by noise in the system. During exponential refractory recovery, the difference between instantaneous threshold and resting threshold at any instant can be stated as a voltage. Firing will occur whenever a superimposed signal (referred to as equivalent noise) exceeds this difference. If time is expressed as frequency, then for any level of equivalent noise there is a corresponding repetitive firing frequency. See text for detailed explanation

Repetitive firing as a function of exponential refractory recovery exemplifies an interesting characteristic of dynamic systems which is often neglected, namely, the role played by noise. Consider, for example, a neuron which has an exponential refractory period having a time constant of 2.7 msec. Theoretically, resting threshold is approached only asymptotically and is reached in an infinite time. Practically, of course, refractory recovery is measured as complete in only a few time constants, generally less than 20 msec. This is true only because of noise in the

system, for instance minute variations in threshold or excitation.

In the case of repetitive firing of the model under d.c. stimulus, the lowest firing frequency is about 50 pps. Just below this minimal stimulus, firing ceases abruptly. The effective recovery time thus is about 20 msec. Since the refractory time constant τ is 2.7 msec, recovery is complete in about 7.5 time constants. What does this imply about noise in the system? Why is the firing frequency not arbitrarily low?

The threshold recovery function, defined as $R(t)$,

$$R(t) = R(1 - e^{-t/\tau}),$$

where R is the threshold increase at the start of the relative refractory period. We can calculate $R(t)$ for different values of t in order to find the extent of refractory recovery at various times. For example at 3τ ,

$$R(t) = R(1 - e^{-3}) = .950 R;$$

recovery is complete to within 5% of resting threshold. If the refractory recovery spans, say 10.5 V (see Fig. 4), then the distance to resting threshold at 3τ is $5\% \times 10.5 \text{ V} = 525 \text{ mV}$. At this point a signal, an uncertainty, or a noise having a magnitude of 525 mV (and the proper polarity) superimposed on the recovering threshold will bring it to the asymptotic (resting) level. A plot of such points, based on a threshold of 1.5 V and a refractory time constant of 2.7 msec, is shown in Fig. 9.

Rather than have an abscissa calibrated in time it is more revealing to indicate frequency. Thus the 3τ point discussed above appears at $\frac{1}{3 \times 2.7} \text{ msec}$ or 123 pps.

The low-frequency cutoff of the neuromime (≈ 50 pps) corresponds to a recovery within 6 mV (0.4%) of resting threshold. Thus, any fluctuation in the "steady" stimulus, or noise in the circuit will cause firing at this time if it exceeds 6 mV. If reliable repetitive firing down to 25 pps is required, then more than $4 \mu\text{V}$ noise may be present, a most unlikely situation.

On the average, the measured peak noise signals at the input in the absence of a stimulus are typically 1.5 mV with occasional peaks of 2 or 3 times the amplitude. The stimulus lead was found to have about 1 mV peak noise on its "steady" signal. This establishes the theoretical low-frequency cutoff between 45 and 50 pps, in good agreement with observed behavior.

This approach may have some utility in the investigation of internal fluctuations in biological neurons. Some experimental and theoretical work has already been done on threshold variations and internal noise (PECHER, 1939; FATT & KATZ, 1952; FRISKOPF & ROSENBLITH, 1958); the technique described above might be used to amplify such results.

Complex properties of the model

In order to exhibit some of the more complicated functions of neurons, external circuits must be appended to the neuromime. Such phenomena as accommodation, adaptation, self-sustained discharge and post-spike polarization may be achieved.

A number of these effects are derived from a unit in which a stimulus both excites and inhibits. It follows from HILL's (1936) proposed internal accommodation process which is dependent upon but which proceeds at a rate different from that of a simultaneous excitation process. HILL showed that any aspects of neural excitability could be rather well accounted for by invoking a time constant k for accommodation and a considerably larger λ for the time constant of dependent accommodation (threshold change).

An equivalent concept can be proposed as follows: threshold remain constant, and substitute inhibition for accommodation. Consider inhibition to be the subtraction of excitation and that linear superposition holds. Since excitability is measured by the difference between excitation and variable threshold in HILL's model, it is equivalently measured by the difference between net excitation and fixed threshold¹ in the alternative view. If the excitation and inhibition mechanisms have appropriate time constants, then the two points of view are identical.

These two equivalent concepts are schematized in Fig. 10. The three sets of curves on the left illustrate the Hill model of accommodation where V is the variable excitation and U is the resultant threshold. Firing occurs only if $V > U$, not therefore present for condition (1), just barely occurring in (2), and lasting the interval shaded in (3).

In the curves on the right, threshold T is fixed. For firing to occur, excitation E less inhibition I must result in a net excitation N which exceeds threshold. Again there is no response in (1), momentary firing in (2) where $N \approx T$, and sustained firing in (3) as long as $N > T$.

Both excitation and inhibition are obtained from stimulus by the circuit of Fig. 11. The inhibition is constant, determined by the choice of R and C , made large compared to the excitation time constant. A number of well-known neural phenomena are produced by using this circuit. They are described in the following sections.

Transient change of excitability. The "accommodation" process described in the foregoing section can be used to simulate many of the well-documented transient excitability phenomena. This follows directly from the fact that a subthreshold stimulus will produce an early and fast reduction in threshold as the excitatory input integrator builds up potential. Consequently, the additional stimulus required during this period to exceed threshold and cause firing is reduced. Threshold subsequently rises (more slowly) to its resting value or beyond as inhibition (accommodation) pervenes.

One method of exploring transient excitability uses a subthreshold constant stimulus. RUSHTON's (1932) results are typical. He showed that during the application of a subthreshold constant current, the amplitude of a brief test pulse required to elicit firing decreases. For the particular nerve tested, this decrease had a sharp onset, reached its maximum value at about 9 msec, and then slowly subsided to initial conditions in 5–10 msec.

¹ Threshold is constant in this view only for prefiring (resting) processes. It is considered to be a variable, however, with respect to the refractory period.

Similar results found in the neuromime are shown in Fig. 12. Each curve was taken for a different constant subthreshold voltage applied at $t=0$. The ordinate value of a given curve at any time is the amplitude of a superimposed 0.5 msec test pulse required

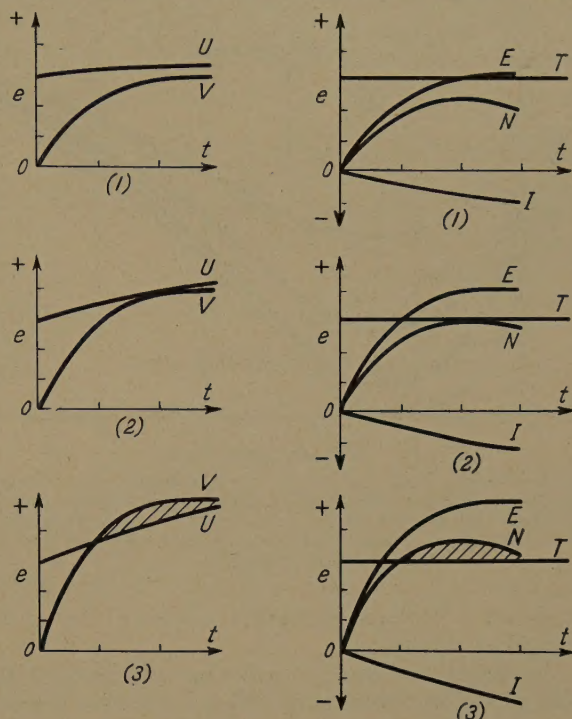


Fig. 10. Equivalent concepts of firing criteria. In HILL's model (left), excitation V must exceed accommodated threshold U for firing to occur. An alternative view (right) assumes a constant threshold. The criterion for firing is that net excitation N exceeds threshold T . Net excitation is the difference between an excitatory stimulus E and a concurrent inhibition I .

to cause firing. One input lead was used ($k = 1.2$ msec), and the time constant of inhibition (analogous to HILL's λ) was 3.7 msec¹.

RUSHTON's curves were asymptotic to resting threshold; no residual accommodation appeared. This

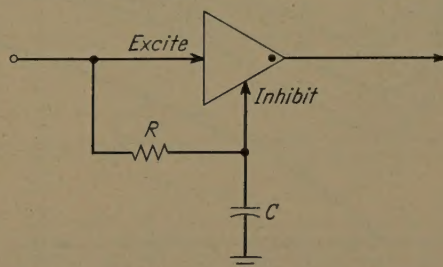


Fig. 11. The circuit configuration used to obtain stimulus-derived inhibition. Part of any stimulus (excitation) voltage is integrated and applied to the inhibition input.

is due to the fact that the conditioning stimulus was removed just after the test stimulus was applied. The curves of Fig. 12 approach a constant inhibition level representing a higher-than-resting threshold; the con-

¹ We adopt the symbol λ for the inhibition time constant. To calculate λ , the 53 K Ω total resistance of the inhibition input circuit (comprising the 24 K Ω resistor and the base resistance of T_5) must be included. For $C = 0.1 \mu\text{F}$ and $R = 120 \text{ K}\Omega$,

$$\lambda = \frac{53 \cdot 10^{-3} \times 120 \cdot 10^{-3}}{173 \times 10^{-3}} \times 0.1 = 3.7 \text{ msec.}$$

conditioning stimulus was left on indefinitely in this case. Any asymptote can be chosen simply by modification of the inhibition network. Similarly the time at which peak excitability occurs also is variable. Rheobase

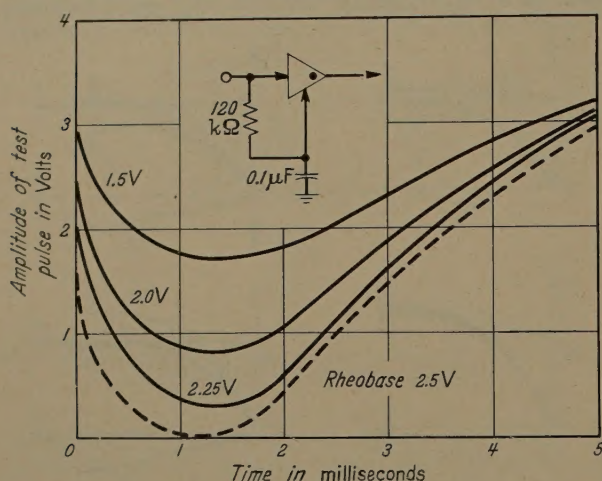


Fig. 12. Transient change of excitability upon the application of a constant subthreshold stimulus. Ordinate values represent the amplitudes required of a 0.5 msec test pulse at various times to cause firing. Maximum facilitation occurs at ≈ 1.3 msec. Each curve represents different levels of conditioning stimulus

becomes 2.5 V for the configuration shown, due to the concurrent inhibition.

Another technique for exploring transient excitability uses a brief pulse rather than a constant current

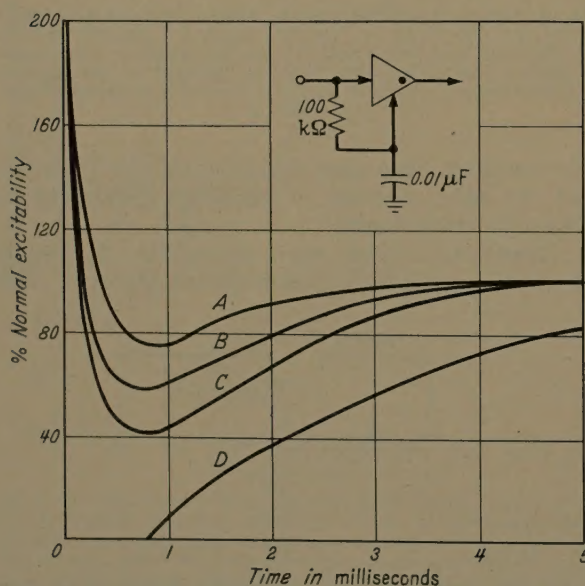


Fig. 13. Transient change of excitability following a 0.5 msec conditioning stimulus. Ordinate values indicate excitability relative to resting threshold (100%). Excitability is established by measuring the amplitude of a second 0.5 msec test pulse required to elicit firing. Threshold is lowered immediately following the conditioning stimulus, passes through rheobase in less than 0.4 msec, and reaches a maximum at ≈ 0.8 msec, gradually returning to its resting value. Curve A results from a low amplitude stimulus; B and C represent increasing levels. In D the stimulus was suprathreshold, thus the time course of excitability follows the refractory recovery characteristic

as a subthreshold conditioning stimulus. This is followed by a test pulse to determine threshold. Typically it has been found (ERLANGER & GASSER, 1937) that the facilitating effect of the conditioning pulse is proportional to its strength, diminishing rapidly after the stimulus is removed. A subnormal phase

follows, having a peak (threshold maximum) at about 0.5 msec for the class of fiber tested, which gradually returns to resting threshold within 3 or 4 msec. Similar behavior in the neuromime follows from the mechanisms operating for a constant conditioning stimulus as described in the preceding section. These changes in threshold have been converted into proportions of excitability and plotted in the curves of Fig. 13. Each point on a curve represents the percent ratio of resting threshold to instantaneous threshold.

A subthreshold conditioning pulse of 0.5 msec duration was terminated at $t=0$, and a variable amplitude test pulse 0.5 msec long was used to determine threshold at a number of time intervals. Curve A was derived from a very weak conditioning stimulus; curves B and C were taken for increasing amplitudes of conditioning pulse. In D, the conditioning stimulus exceeded threshold and the unit fired. This curve therefore represents refractory recovery. These results closely parallel those of ERLANGER & GASSER. Recovery in each case is to resting threshold (100% excitability) since there is no long-lasting stimulus to maintain accommodation.

Pulse trains. For a stimulus of indefinite duration whose level is above threshold but below some critical value, a burst of output pulses will occur for a time during which accommodation has not yet overtaken excitation (HILL, 1936; KATZ, 1936; HODGKIN, 1948). KATZ demonstrated a linear relation between the logarithm of relative excitation ($\ln I/I_0$) and burst duration, obtaining a family of such lines for various accommodation time constants λ .

This behavior in the neuromime also follows directly from the stimulus-derived inhibition described above. The results shown in Fig. 14 closely approximate those described by KATZ.

The measured average excitation time constant was 1.0 msec for the units tested; this value was maintained for all results described below. The inhibition time constant λ was adjusted by varying C (Fig. 1) from $0.5 \mu\text{F}$ ($\lambda = 21$ msec) to $5.0 \mu\text{F}$ ($\lambda = 210$ msec) holding R constant at $200 \text{ K}\Omega$. It is seen that the burst duration is a linear function of $\ln E/E_0$ where E is the stimulus level used to elicit the burst and E_0 is the rheobase. As KATZ pointed out, HILL's results imply that the relationship of burst duration to stimulating current, threshold, and excitation and accommodation time constants is

$$e^{t/\lambda} = \frac{I/I_0}{1 - k/\lambda}$$

and if $k/\lambda \approx 0$, as is found in nerves showing repetitive response, then

$$t \approx \lambda \ln I/I_0.$$

This is the result obtained from the model and plotted in Fig. 14. We expect to find that when $I = \epsilon I_0$, $t = \lambda \ln \epsilon$. The points shown in the figure are located at the expected values. The measurements were made for voltages E rather than for currents I .

Burst duration lengthens as excitation is increased to a critical level, beyond which sustained firing occurs. This occurs because the inhibition circuit saturates at a somewhat lower level than does the excitation circuit. Consequently at very high stimulus levels steady-state net excitation is above threshold, and the burst becomes indefinitely long.

Increased duration of burst implies greater numbers of pulses per burst, since frequency of firing also goes up with increased excitation. The discrete steps observed in this process are shown in Fig. 15A.

For an inhibition time constant of 5.2 msec there are only four levels before sustained firing occurs. As λ is increased so that accommodation lags more and more, greater numbers of levels occur.

In Fig. 15B it is seen that for $\lambda = 210$ msec, bursts more than 110 pulses occur. Individual steps have not been plotted for these curves beyond the first few levels. Sample points were taken at the higher levels and smooth curves drawn for simplicity.

For an excitation time constant which is short relative both to typical interpulse periods and to inhibition time constant, net excitation rises quickly and

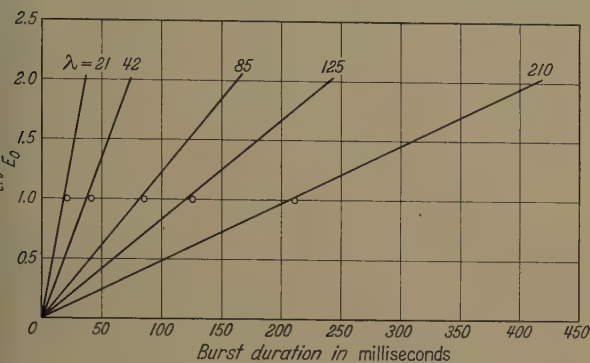


Fig. 14. Relation between multiple-response (burst) duration and relative excitation for various time constants of inhibition (accommodation). The points shown are theoretically predicted values of burst length when the excitation E is ϵ times the rheobase E_0 .

subsides slowly. This results in adaptation which consists of a high initial firing frequency which diminishes as the burst progresses. When output frequency is measured as a function of time for several different inhibition time constants, the curves of Fig. 16 result. Each of these curves was derived from a constant applied stimulus $7.4 \times$ rheobase, ($\ln E/E_0 = 2$), hence they all start at essentially the same frequency. The form of each curve is exponential, reflecting the exponential course of the growing inhibition. Firing ceases at about 50 pps, the low frequency cutoff described earlier and shown in Fig. 7.

Examination of the total number of pulses in a burst for each value of λ suggested a relationship which has not been previously obvious. As shown in the curves of Fig. 17, it appears that the pulse number is a linear function of inhibition time constant. This holds over a wide range of stimulus levels. Curve A results from $\ln E/E_0 = 2$; in B , $\ln E/E_0 = 1.5$, and C represents the condition $\ln E/E_0 = 1.0$.

That this relationship must hold is evident if the functions shown in Fig. 16 are considered more carefully. Since each curve represents firing frequency f as a function of time, the area under each curve must equal to the total number of pulses, N . That is,

$$N = \int_0^T f(t) dt. \quad (5)$$

The net excitation available to the neuromime is the stimulus-derived excitation less the stimulus-derived inhibition. In the circuit used, these two components are approximately equal¹ so that in the

¹ This is equivalent to HILL's (1936, p. 319) assumption that $U_1 - V_1 = U_0 - V_0$.

steady-state the net excitation lies just below threshold. Both excitation and inhibition are exponential functions; thus, net excitation

$$E(t) \approx E_{\max} (1 - e^{-t/k}) - E_{\max} (1 - e^{-t/\lambda}) \quad (6)$$

where $E_{\max}$ is the stimulus amplitude, and k and λ respectively are the excitation and inhibition time constants. For the production of bursts, accommoda-

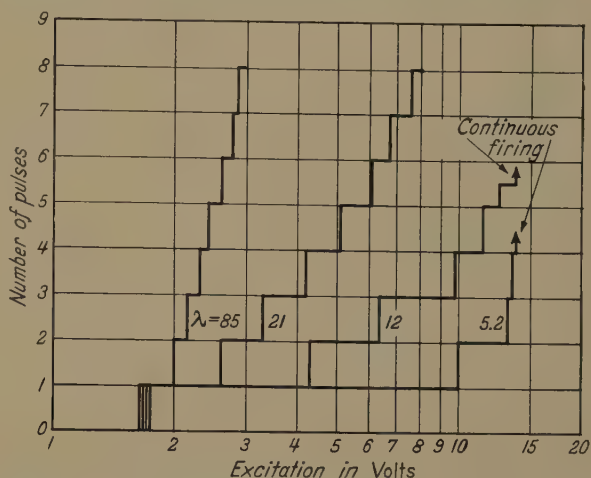


Fig. 15A. The number of pulses in a transient burst increases with excitation and with inhibition time constant λ . Above a critical stimulus level, continuous firing occurs.

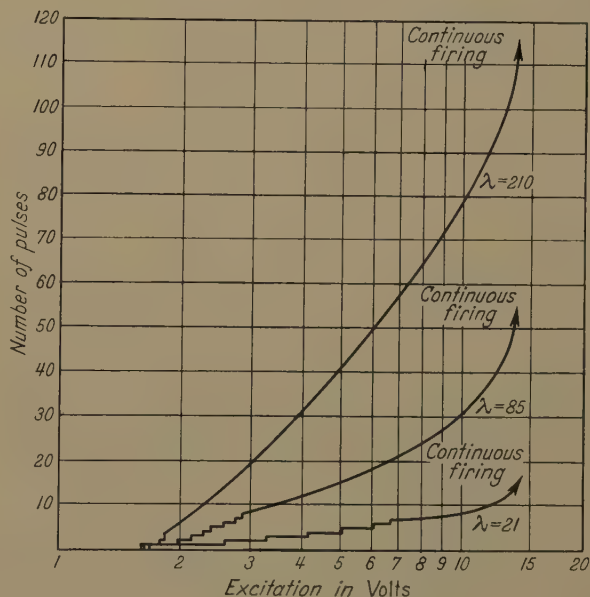


Fig. 15B. The number of pulses in a burst as a function of excitation for large values of λ . Smooth curves rather than discrete steps have been drawn for simplicity where the pulse count becomes large. Over 110 pulses have been observed in a burst for an inhibition time constant of 210 msec.

tion must rise much more slowly than excitation, hence for the case of interest $k \ll \lambda$. Hence Eq. (6) can be simplified to

$$E(t) \approx E_{\max} e^{-t/\lambda}. \quad (7)$$

From Fig. 7 we have the approximate relationship

$$f(t) = cE(t) \quad (8)$$

where $f(t)$ is instantaneous frequency and c is a constant of proportionality. Thus we can rewrite Eq. (5), the expression for the sum of the pulses, as

$$N \approx c \int_0^T E_{\max} e^{-t/\lambda} dt \quad (9)$$

$$\approx cE_{\max} \lambda (1 - e^{-T/\lambda}). \quad (10)$$

T is the time at which firing ceases. This occurs at a definite firing frequency, f_c , which is the same for all λ (about 50 pps) as shown in Fig. 16. Hence from Eqs. (7) and (8)

$$f_c \approx cE_{\max} e^{-T/\lambda}. \quad (11)$$

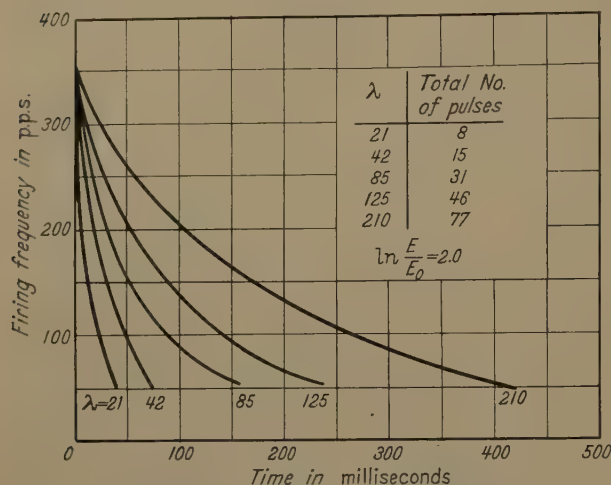


Fig. 16. Adaptation during a burst for various inhibition time constants. A step-function stimulus of $7.4 \times$ rheobase causes initial firing rates of ≈ 350 pps in each case; concurrent inhibition supervening at a rate dependent on λ eventually terminates each burst at ≈ 50 pps, the low-frequency cutoff

Substituting (11) into (10), we have

$$N \approx \lambda (cE_{\max} - f_c).$$

Since c , $E_{\max}$, and f_c are constant,

$$N \propto \lambda, \text{ approximately.}$$

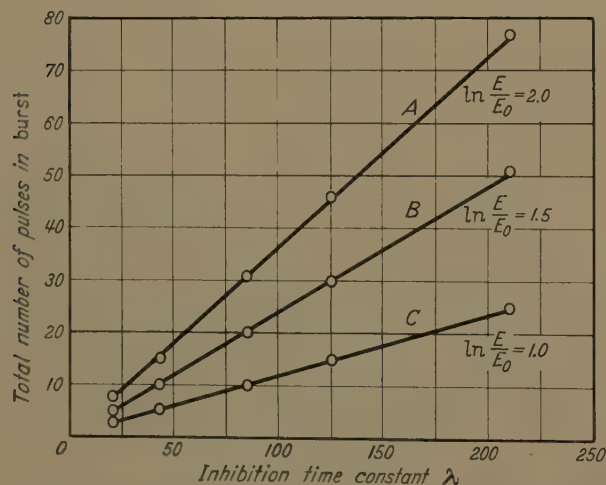


Fig. 17. The total number of pulses in a transient burst is a linear function of the inhibition time constant for any given stimulus level. A results from a stimulus E where $\ln E/E_0 = 2$. In B, $\ln E/E_0 = 1.5$; in C, $\ln E/E_0 = 1.0$. This is predictable from the nature of the time course of the stimulus-derived inhibition. See text for detailed analysis

The approximate nature of the relationship arises from the nonlinear firing frequency characteristic, the fact that final net excitation is not exactly zero, and the fact that k is not vanishingly small. For the cases considered, the approximation is accurate to within 5%, hence with this limitation we can write

$$N \propto \lambda, \quad (12)$$

that is, the total number of pulses in a burst is directly proportional to the inhibition time constant. The closeness of the approximation is evident in the linearity of the curves in Fig. 17.

It would be interesting to know if this result can be verified experimentally for biological preparations.

It is implicit in the work of KATZ and in the exponential nature of accommodation, as was shown above. Confirmation could be useful, since counting the number of spikes in a burst may provide an index of accommodation time constant more easily obtained than by the use of conventional experimental techniques. It should also be noted that for the conditions discussed, adaptation mirrors accommodation; their time courses are identical. Hence in this case the accommodation time constant can be inferred from measurement of adaptation.

By varying the inhibition parameters (level and time constant), a wide range of accommodation and adaptation can be exhibited. Without inhibition, no accommodation and no adaptation occurs; rheobase stimulation elicits repetitive discharge which is constant in frequency. For moderate inhibition, as described, rheobase stimulation elicits one or two pulses. Increased levels of stimulation evoke bursts or repetitive discharges which exhibit accommodation and adaptation. This variety of behavior is seen in the results described by HODGKIN (1948) for a large class of motor neurons and sensory receptors.

Self-sustained discharge. There are two basic kinds of mechanisms which can give rise to continuous activity (i.e., oscillation) in the absence of external stimulus. In one, a closed chain of neurons propagates reverberatory activity around a loop (LORENTE DE NÓ, 1949). The minimum number of units required in the loop is determined by pulse amplitudes and durations and by refractory time constants. Any given unit must recover sufficiently before the next stimulus comes along.

The second class of self-sustained oscillators depends on positive feedback around only one neuron. This feedback may be due to internal mechanism or to a feedback loop around the entire unit, as may occur in recurrent axon collaterals. An output-derived potential in the neuromime can easily be integrated and fed back to form an adequate excitation stimulus for self-sustained discharge. In this case, maximum firing frequency is limited by the refractory time constant and the available output level.

The two kinds of circuits are shown in Figs. 18 and 19. In Fig. 18, where curve A is for one excitatory input lead, a minimum of seven units is required for oscillation. As more units are added, oscillation continues, but because transit time through the loop increases, firing frequency decreases. If all five input leads are strapped together (curve B), the more effective excitation causes firing earlier in the recovery cycle; hence fewer units and higher frequencies are possible.

In this type of self-sustained discharge circuit, the upper firing frequency is determined by the transit time in the shortest possible loop. There is no limit on the lowest firing frequency; this is determined solely by the total number of units in the loop.

In the single-unit oscillator of Fig. 19¹, the firing frequency is independent of C as C is made large.

¹ Note how this circuit differs from that of Fig. 8. In both circuits a potential derived from the output is fed back to an input. However, in the case of the oscillator (Fig. 19) the feedback is positive; an output signal is applied to the excitatory input. This action is regenerative. In contrast the circuit of Fig. 8 utilizes negative feedback since the output applied to the inhibitory input, tends to depress further activity.

sufficiently large capacitor insures a fully smoothed output waveform. That is, the output pulses are integrated to yield a feedback excitation voltage which is relatively constant, being the peak amplitude of the output pulse. As C is decreased, the average feedback voltage is diminished, and firing frequency drops off until available excitation does not exceed instantaneous threshold. Thus the lowest possible firing rate for this type of reverberatory circuit is fixed, unlike the multiple unit loop circuit. The upper limit of firing frequency, which is determined by the peak output voltage, is likewise bounded.

Curve A depicts the case for three input leads clapped together. Oscillation becomes impossible if more leads are connected in parallel, i.e., if the input time constant k is made smaller than 0.66 msec. There are two reasons for this. As k is reduced, latency is increased. Hence excitation derived from an output pulse occurs earlier, when refractory recovery is less complete. Secondly, reducing k means that C is discharged sooner, with the result that the feedback excitation is drained more rapidly. Curve B results from using one input; here latency is increased, hence the repetition rate is lower.

A special case of summation. During the course of these experiments an unusual and unsuspected phenomenon was found. It may have no relevance to biological behavior, but it does illustrate an interesting additional property of neuron-like entities.

If one unit is used to drive another directly, and the pulse amplitude is sufficiently high, then one would expect the second to "follow" the first, pulse for pulse. This is, in part, what is observed. At relatively high frequencies, however, the second unit begins to "drop out"; i.e., at some point the pulse amplitude of the first is insufficient to exceed the relative refractory threshold of the second. But if three (or more) of the excitatory inputs of the second unit are strapped together to utilize the driving pulses more effectively, then following is complete up to the maximum possible firing rate. This action was mentioned briefly in an earlier section dealing with delay.

Consider now the following experiment. Suppose that at some relatively high frequency (say 400 to 500 pps) one unit is following another, pulse for pulse. Each one-for-one following has been described by BULOCK (1946) and by FURSHMAN & POTTER (1957). Now let the output amplitude of the driving unit be monotonically reduced, "starving" the driven unit. This could represent a case either of decremental conduction of spikes or a change in threshold of the recipient neuron. As the driven unit receives progressively less excitation, there will be a critical point at which a given driving pulse has insufficient energy to fire the driven unit. However, it turns out that when the next driving pulse comes along, it is integrated with the preceding one to cause firing. In other words, temporal summation occurs, and the firing frequency of the driven unit is half that of the driver. One could expect that as the driving pulse amplitudes are reduced still more, every third pulse would be effective, then every fourth¹ etc., so that f_1/f_2 which

was originally unity, progresses integrally 1, 2, 3, 4, ... This is what one reasonably expects to happen, but in fact it does not. What does occur is shown in Fig. 20. The ratio of f_2/f_1 has been plotted for convenience. It is seen that for decreasing excitation at the second unit, the integral steps expected show up, but considerably more complex behavior also appears. Thus the predicted steps are seen as 1:1, 1:2, 1:3 ... 1:10 (frequency division has been ob-

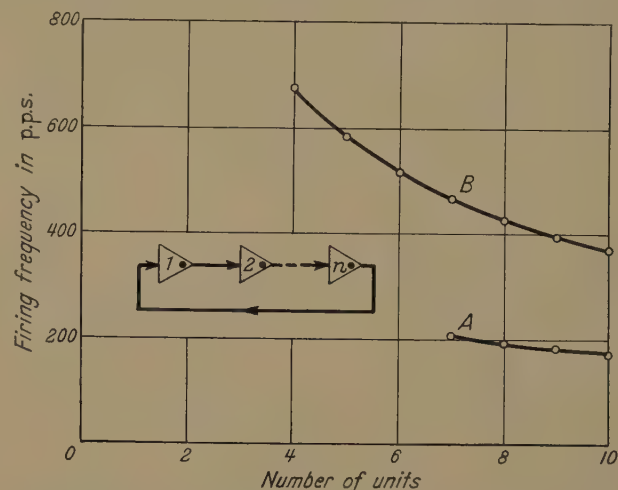


Fig. 18. Self-sustained discharge in a chain of N units. A minimum of 7 is required when a single input lead is used (A). With more effective excitation obtained by five input leads in parallel (B), only 4 units are required to sustain oscillation. In each case, as more units are added to the chain, firing frequency diminishes

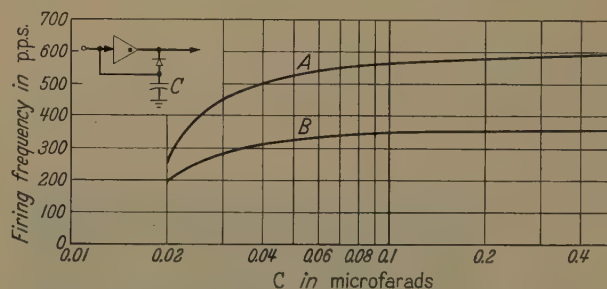


Fig. 19. Self-sustained discharge obtained by a feedback loop around one unit. Increasing the output-pulse integrating capacitor provides a greater average level of self-excitation. Firing frequency thus increases up to the limit imposed by the maximum available output-pulse amplitude. Oscillation becomes impossible when the filtering is inadequate to maintain sufficient stimulus level

served up to 1:13). However a much larger number of nonintegral steps (such as 3:5, 5:16, 3:19, etc.) also appears. This cannot be explained simply on the basis either of summation or refractory recovery alone or in combination.

It was found that the mechanism responsible for this curious behavior depends on phase relationships

recovery additionally comes into play. Note that a pulse in such a continuous train of reduced amplitude pulses fails to excite because it is subliminal with respect to instantaneous (refractory) threshold, not to resting threshold. Hence some subsequent driving pulse will elicit firing when refractory recovery has progressed sufficiently. Therefore the 4th, 5th or n th pulse in a train can be effective. In this way a pulse frequency division occurs, every n th driving pulse causing the driven unit to fire. "Summation" can then be considered as a composite process; classical axon summation occurs for nonrepetitive stimuli, where each of a few subthreshold pulses are integrated to exceed quiescent threshold. In the case of repetitive stimuli, $n-1$ pulses in each train of n pulses fail to exceed the instantaneous dynamic threshold; this is iterated subtraction, i.e., division.

¹ Summation becomes ineffective for more than n pulses when the time from the first to the n th pulse exceeds the effective integrating time at the input of the driven unit. Typically this limit is 2 or 3 pulses. However, refractory

between pulses in both N_1 and N_2 . This can be seen in Fig. 21.

The top line shows the output of the driving unit. Seven down-going pulses appear. The bottom row of

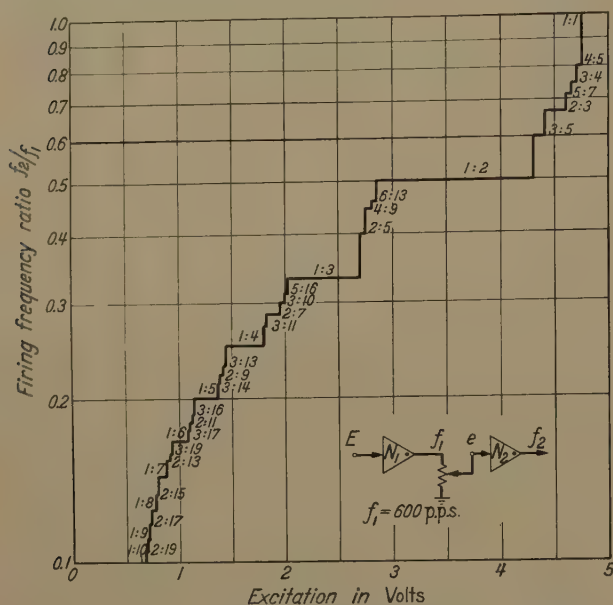


Fig. 20. Firing response of one unit being driven by another. "Following" is precise at high levels of excitation. As the driven unit receives progressively smaller stimuli, it begins to drop pulses. The 1:2 and 1:3 steps result from ordinary temporal summation. Other ratios of firing frequencies stem from another phenomenon, caused by asynchrony between driving pulses and the refractory period of the driven unit

pulse represents the output of the driven unit. Note that, including the partial pulse at the right end, only six appear. One pulse, corresponding to the fifth one from N_1 has dropped out. This sequence repeats (not

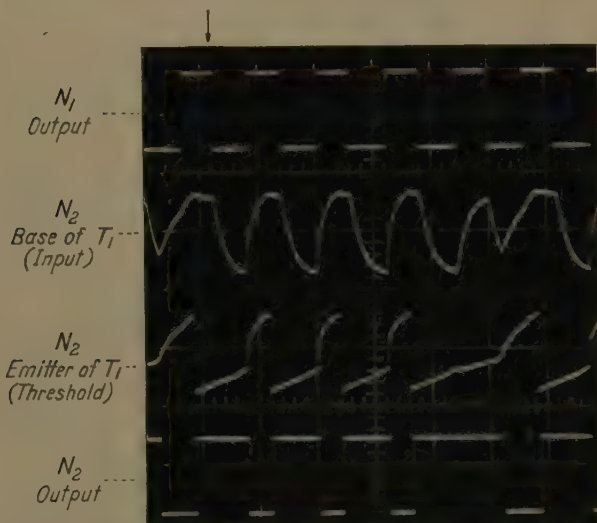


Fig. 21. Phase relationships between driving and driven units which explain the firing frequency relationships of Fig. 20. See text for detailed explanation

shown) in such a way that there are only 4 pulses from N_2 for every 5 pulses from N_1 . This corresponds to the 4:5 step shown in Fig. 20.

The reason for this behavior can be seen by considering the second and third traces of Fig. 21. In the second, the base of T_1 (input transistor, see Fig. 1) in N_2 reflects the (integrated) input pulses coming from N_1 . Consider the second pulse as a starting point,

as indicated by the arrow. The voltage at the base of T_1 in the driven unit falls exponentially to a particular level as the pulse from N_1 charges up the input integrating capacitor. Meanwhile the emitter of T_1 (3rd trace) rises from a deep, fully inhibited level heading for the resting threshold level at a rate governed by the relative refractory time constant (the unit is just recovering from having been fired by the previous N_1 pulse). At the time that the potential at the base of T_1 is equal to the potential at the emitter, the firing threshold condition is satisfied, and an output pulse in N_2 is initiated. This occurs just before the end of the second N_1 pulse. The base of T_1 reflects this firing by terminating the input pulse integrating process and by being rapidly pulled in the positive (upward) direction.

At termination of the output pulse, the base of T_1 is again free to integrate the next pulse out of N_1 . Meanwhile the relative refractory phase, reflected in the slow rise of potential on the emitter of T_1 , has begun again as soon as the N_2 output pulse terminates. Note, however, that as this action repeats, the time at which N_2 fires becomes progressively later with respect to the N_1 driving pulse. This follows from the fact that the instantaneous magnitude of the N_2 threshold (refractory curve) is not phase-locked to the N_1 driving pulses. Thus a phase slippage can and does occur. Eventually (at the fifth pulse) this slip accumulates to the point that by the time the driving pulse ends (the base of T_1 has reached its maximum excitation level), the refractory recovery has not been sufficient to allow firing. Consequently a pulse is missed.

Refractory recovery continues during this blank interval, more and more closely approaching resting threshold. Then the next N_1 pulse comes along. Since the threshold is now quite low, firing occurs relatively early. Again the base of T_1 is discharged and awaits the next input signal. Thus the cycle is completed, this point in time corresponds to the situation at the second pulse where the tracing of the sequence began.

It would be interesting to examine biological preparations for the presence of this type of coding. Auditory volleying, for example, may utilize such mechanisms.

Uses for the model

There are two distinct types of explorations which can be made with the described model. In one, single unit properties can be studied in detail, and new or unsuspected relationships may be suggested or disclosed. Such characteristics as the linear relation of number of pulses in a burst to accommodation time constant, and the "summation-division" pulse-following function are examples of such results.

At a higher level, group interaction properties such as the behavior of small networks and transducer encodings, for example, may be studied. It has been possible to explore systems at the retinal and cochlear levels with profit (VAN BERGELJK & HARMON, 1960). Such mechanisms as on, off, and on-off receptor systems, and dynamic range extension in spiral innervation networks have been examined with these electronic models. Other studies have been made of the possible neurological origins of flicker-fusion phenomena and of primitive pattern recognition.

The two papers following describe in detail two these explorations. Current and continuing work intended to elucidate further some of the information-processing mechanisms of peripheral neural structures.

Increasingly detailed knowledge of neural functions made more and more complex our picture of the neuron. In a very real sense a unified and comprehensive understanding appears to become more, rather than less, remote. However, it may very well be possible that a small number of basic properties accounts for the essential computing functions of this element. Certainly to a first-order approximation the characteristics discussed in this paper underlie much observed neural activity. A small number of primitive relationships describe a large body of experimental results.

In the design of the electronic model, a few simplified *a priori* assumptions were seen to have implicit in them many functions of biological neurons. Consequently, a fundamental theory of neural action may ultimately be much less complicated than the enormous body of detailed study presently leads one to suspect. A simplified, coherent view of neural events is highly desirable; neural analogs can provide a useful tool in approaching that goal.

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Studies with Artificial Neurons, II: Analog of the External Spiral Innervation of the Cochlea

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With 10 Figures in the Text

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Summary. 1. Artificial neurons (neuromimes) are used to simulate the external spiral innervation of the cochlea.

2. On the basis of the experimental observations the proposition is advanced that the spiral innervation serves to extend the dynamic range of the ear. Dynamic range extension follows from elementary considerations of the refractory and summing properties of nerve fibers.

3. Experiments with different neuromime densities, supported with psychophysical observations reported in the literature, lead to the hypothesis that dynamic range and growth of sensation are related to the innervation density in the area of sensory tissue under consideration (e.g., skin). The spiral nerves are considered as a special case of a more general sensory nerve, branching in binary fashion.

4. The pathological phenomenon of "loudness recruitment" is explained as a "thinning" of cochlear innervation density, giving rise to smaller dynamic range and faster growth of loudness.

Introduction

The innervation of the cochlea, according to LORENTE DE NÓ (1937) and FERNÁNDEZ (1951) can be

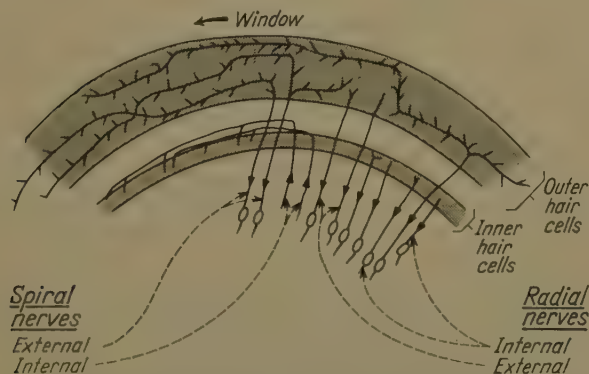


Fig. 1. Schematic drawing of the innervation of the cochlea; a segment of a turn is represented. Black arrows indicate direction of transmission. After LORENTE DE NÓ (1937) and FERNÁNDEZ (1951)

divided into four groups (see Fig. 1): 1. The internal radial fibers connect directly to one, or to very few, internal hair cells. 2. The external radial fibers, which cross the arch of CORTI, also connect to one or to a few external hair cells. 3. The external spiral fibers cross the arch of CORTI, course underneath the external hair cells and connect through side branches to numerous outer hair cells. 4. The internal spiral fibers run in the tunnel of CORTI and connect with side branches to many inner hair cells. This last type of innervation is thought to be efferent (the other three are presumably afferent) and seems to be the terminal point of the bundle of OORT and the tract of RASMUSSEN (Olivocochlear tract).

Of the other three types of (afferent) innervation, the least seems to be known about the external spiral fibers, both as to anatomy and to function. LORENTE DE NÓ states definitely that the spiral fibers run in the direction of the base of the cochlea. FERNÁNDEZ (1951) believes that this is only partly true; he finds that there are many fibers which run in the opposite direction; a number of fibers even appear to split up and send branches in both the apical and basal

directions. HELD (1926) shows the fibers in his pictures as running predominantly in one direction, but fails to state which direction this is.

The anatomists are not in agreement on the length of these fibers ("as much as one third turn" — LORENTE DE NÓ; "a quarter turn" — HELD), and they are even less definite about the number of side branches of the hair cells innervated ("numerous" — LORENTE DE NÓ). About the function of this type of innervation, more than speculation exists. DAVIS (1952) thinks "it may allow spatial summation of weak local excitatory effects when the cochlea is stimulated by very faint sounds".

This paper will trace a line of thought and present some model experiments which lead to an hypothesis about the function of the spiral innervation.

Logical properties of nerve branches

It is beginning to be well known now that at bifurcations of nerve fibers, especially axonal terminations and arbors, there exists a certain probability that a propagated impulse fails to pass into one or the other or even both branches (WALL, LETTVIN, MCCULLOCH and PITTS, 1956). This conduction failure seems to be purely statistical, i.e., it is not possible to state whether a given impulse will pass or fail. We may think of this behavior as characteristic of divergent neural arborizations.

There are, however, also convergent neural arborizations such as the external spiral innervation and the sensory innervation of the skin. Here (Fig. 2) conduction of impulses is in a direction opposite to that in the divergent arbors. In this case, however, it is possible to state accurately when conditions are sufficient to cause blockage of a particular impulse. Consider the junction point J in Fig. 3. Here branch-fibers A and B join to form fiber C. Suppose an impulse from A has just passed through J; now J will be refractory for a short time, and an impulse arriving at J from B will be blocked. It may also lengthen the refractory time such that the next impulse from A can be blocked, and so forth, the sort of phenomenon perhaps responsible for Wedensky inhibition. The diminished amplitude of an impulse arriving at an incompletely recovered section of nerve fiber may cause failure of this impulse (see, for example, the phenomenon of nonintegrative division discussed by HARMON in the preceding paper).

It may be argued that there is no reason why the impulse from A should not antidromically invade B as well as go orthodromically into C. On closer inspection, however, it is seen that an invading impulse would make B refractory for a time amounting to the total travel time of the impulse in B plus B's effective refractory time. Effectively, then, the refractory period of J is extended by this amount of time for an impulse originating in the sensory cell of B. Since the junction of branch B and its hair cell is presumably synaptic, the antidromic pulse would not affect the (presynaptic) excited state of the hair cell. Since

assumed to be short, the total effective refractory time of J with regard to B is perhaps a factor of two or three greater than local measurement at J would indicate. Meanwhile though, J's refractory time with regard to A remains at this "local", lower value, and the probability of passage of an impulse from A is differentially enhanced. Although this suggests an interesting mechanism for "neural funneling" (VON KÉSY, 1958, 1959), we will not be concerned with it here.

Clearly, the amount of blocking at J is closely tied to the frequency of impulses in A and B. If both branches are firing at a very low rate, say around five per second, and the firing epochs are randomly distributed, the probability of interference is small. This may be better expressed reciprocally by saying that the probability of addition of A and B into C is great. At the other end of the scale, A may be firing at saturation level, i.e., impulses are conducted in as high a frequency as the refractory time constant will allow. In that case, it would be impossible for the other branch B to interpolate impulses, and the probability of addition reaches zero. However, as pointed out earlier, impulses in B may lengthen the refractory time of J, and so block pulses from A. Thus, the probability of addition may become negative, i.e., subtraction can take place. Although this mechanism seems to lend itself quite naturally to formal analysis, there does not appear to be a mathematical tool to handle it conveniently; especially, long chains of these junctions, where C and another branch D converge at junction I to form E, etc. may be difficult to manage.

For this reason, it was decided to simulate the internal spiral innervation by means of simple nerve analogs. HARMON in 1959 and in the preceding paper described such analogs. Most of the experiments to be reported here were done with the earlier model, although all results were checked with the later models as well. Apart from scale factors, results were identical. The printed circuit cards on which these "neuromimes" (VAN BERGELJK, 1960) are realized are easily assembled into modules with patch cord connections, each unit incorporates primitive properties believed to be characteristic of nerve fiber: threshold, temporal summation, all-or-none response, firing rate related to excitation intensity, absolute and relative refractory periods and transmission delay.

Experiments

Fig. 4 shows a diagram of the measuring set-up. The "Basilar membrane" used here is the electrical analog of the cochlea built by BOGERT (1951). This network has a large number of taps, permitting observation of the displacement pattern (here voltage pattern) in intervals corresponding to 0.2 mm along the actual basilar membrane.

The outputs of ten selected taps were amplified and rectified (frequencies of stimulation much higher than any frequency the neuromimes could respond to directly were used); to protect the neuromimes from breakdown, the outputs from the rectifiers were limited to 45 volts. The selection of the taps involved decision on how much space to allow between them and in which "turn" of the network to place them. In most of the experiments to be described, the distance between taps was equivalent to 2 mm, going

from a point corresponding to 8 mm from the stapes to a point equivalent to 26 mm from the stapes, thus covering most of the basal and all of the second turn

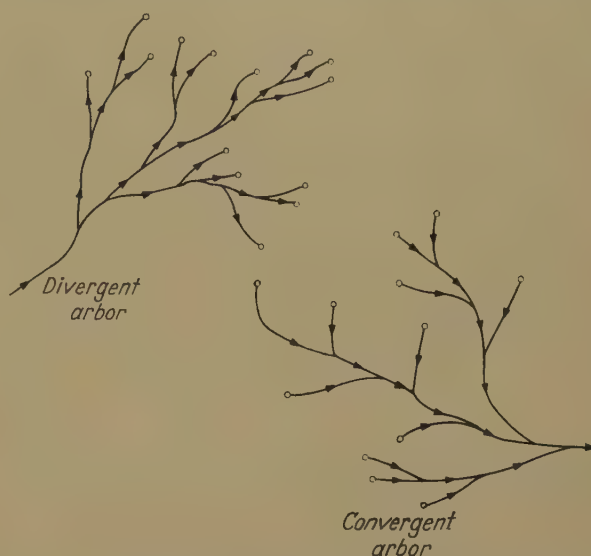


Fig. 2. Trees in the nervous system. Divergent arboris are usually axonal, convergent arboris commonly dendritic terminals

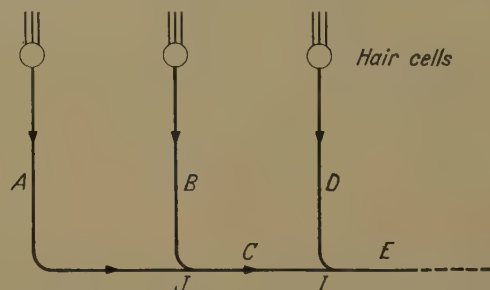


Fig. 3. Diagram to explain behavior of spiral nerves; see text

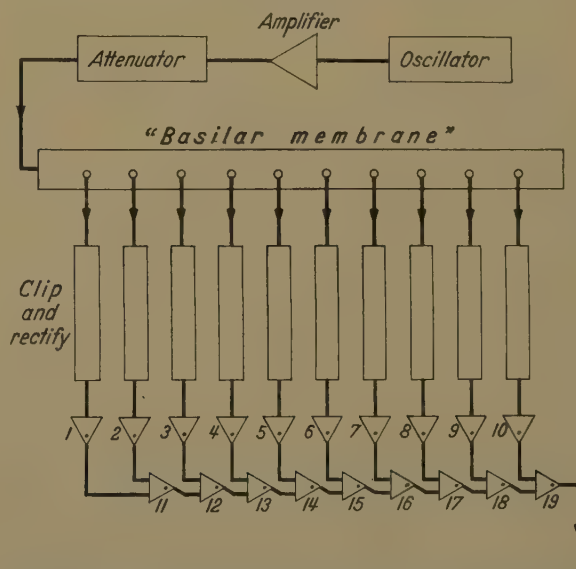


Fig. 4. Diagram of experimental set-up. The "basilar membrane" is the analog network of BOGERT (1951); the numbered triangles represent the neuromimes making up the simulated spiral nerve

of the analog cochlea. This is considerably more than the "one-third of a turn" length of the spiral fiber estimated by LORENTE DE NÓ. It turns out, however, that the results are qualitatively unaffected by variations in the distribution, as we shall see shortly.

Let us consider one of the several experiments that were done. Suppose the nerve runs toward the apex, and its branches are ten in number, evenly spaced at 2 mm intervals, as outlined above. Fig. 5 shows this situation; superposed on it is the envelope of a traveling wave of 1000 cycles. This envelope is proportional

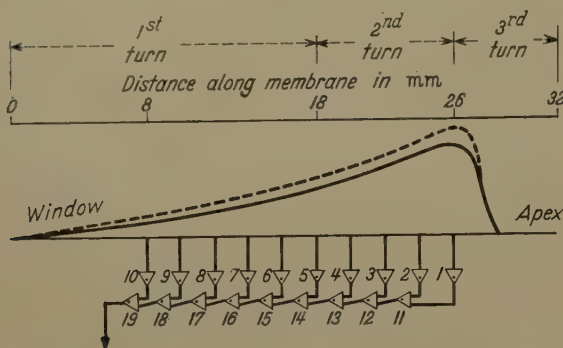


Fig. 5. A typical experiment, as discussed in the text, consists of a "nerve" coursing toward the apex and spanning part of the first and the whole second turn of the analog cochlea. The solid and dashed curves represent the voltage patterns on the "cochlea" for different intensities of input sine-wave.

to the rectified voltage obtained from the taps. The output of a neuromime is a train of pulses; the frequency of the train is monotonically related to the input voltage. Since neuromime 1 in Fig. 5 is closest to the envelope maximum, it will be stimulated supraliminally before any of the others as the intensity of

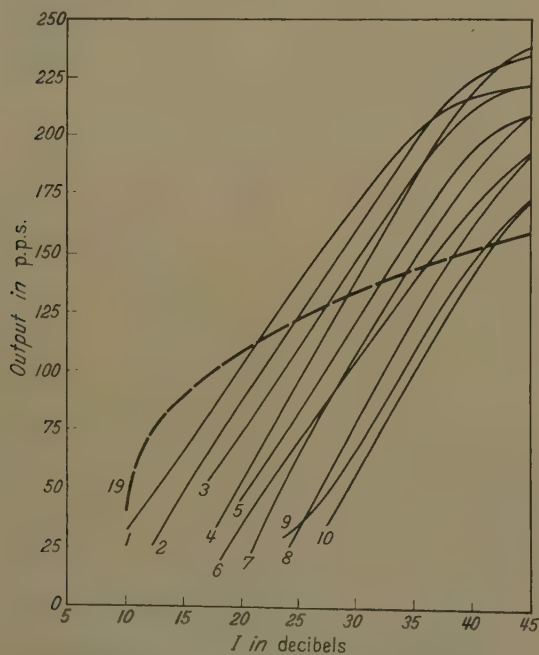


Fig. 6. Results from experiments such as pictured in Fig. 5. The curves are averages from several experiments

the stimulus (1 KC sine wave) is increased. Let us assume that the solid-line envelope of Fig. 5 represents this condition; only neuromime 1 is active at its lowest stable rate. As intensity is increased, neuromime 2 becomes active at threshold (dashed envelope in Fig. 5). As intensity is further increased, all neuromimes in turn become activated, but by the time neuromime 10 is producing some 100 pulses/sec., neuromime 1 is approaching saturation, i.e., it is firing close to its maximum frequency (225 pulses/sec.). Fig. 6 illus-

trates the process; input intensity in db is plotted vs. output firing frequency in pulses per second. The particular amplifier used did not deliver more than 45 db gain. Note that the curves do not run precisely parallel; the characteristics of the neuromimes show individual variations; biological neurons presumably show similar variability. Typically, however, a single neuromime goes from threshold firing to saturation firing in a 20–25 db range. This happens to be just slightly more than the range covered by real nerve (KATSUKI, SUMI, UCHIYAMA and WATANABE, 1958). When we look at the output of the composite 10-branch fiber (here the output of # 19), we see that the response is graded over a much larger range. In other words, the *dynamic range of the system has been extended*. In our model it is possible to look at intermediate locations of the "fiber" as well as at the last output. Fig. 7 shows the results; the shorter the chain of side branches, the steeper is the slope of the line relating input intensity and output frequency, until of course the limit is reached when there is only one sidebranch left. From this result, we may advance the suggestion that the *dynamic range of a spiral nerve fiber is directly related to its number of side branches or to the number of sensory cells innervated by the fiber*. Conversely then it might be possible to estimate the number of side branches from the slope of the intensity-frequency curve. Of course, it is impossible to record from different spots in the living spiral fiber; only the final nerve (somewhere in the eighth nerve bundle) is accessible. However, the basilar membrane has the convenient property that the traveling wave envelope treats as the frequency of the tone is increased, thus rendering more and more sidebranches inactive. Effectively, increasing the frequency shortens the active part of a spiral fiber, thus generating progressively steeper slopes of the intensity-output curves. Hopefully, one may be able to record such data from animals but unless the branches are rather far apart, quantum steps corresponding to silencing of single branches may not be noticeable. It should be possible, however, to deduce the length of a spiral fiber by noting at which frequency the intensity-output slope does not decrease further (apical end of fiber) and at which frequency no response at all can be obtained (basal end of fiber). Since the displacement pattern of the basilar membrane is known with some accuracy, the absolute position of the fiber can be estimated.

In the experiment just discussed, the direction of the fiber was toward the apex; experiments were also done with the fiber running to the base and with "split" fibers. The most striking result of those experiments was that the direction of the fiber does not matter, as far as the eventual output from the whole nerve fiber is concerned. In other words, the slope of the intensity-output curve from neuromime 19 (or 18 in the "split" case) was the same for all configurations as long as the sidebranches were connected to the same taps on the analog basilar membrane. This leads to the suggestion that the *dynamic range of the fiber is invariant under topological distortion of its course*. There is, however, a difference in the way the curve changes as the number of branches is reduced. This is illustrated best by a comparison of Figs. 7, 8, and 9. Fig. 8 presents results from a fiber running toward the base, Fig. 9 is from a split fiber. Note that in Fig.

shorter chain data "peel off" downward, as opposed to the upward peeling of Fig. 7. Fig. 9, illustrating the split fiber case, shows both modes.

As mentioned earlier, most of the experiments were done over an unrealistically large segment of the log-cochlea; the reason for this was that the responses could be more clearly interpreted. Some experiments were done, however, with a chain of 19 neuromimes extending from a spot corresponding to 19 mm from the stapes to a position corresponding to 19 mm from the stapes, or about half of the first. The curves obtained are much smoother than those obtained from the coarser distribution, but

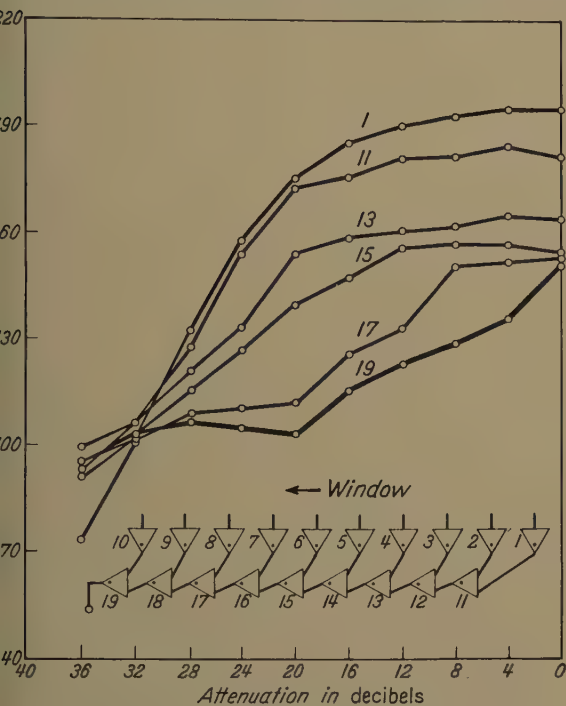


Fig. 7. Sample curves from an experiment as depicted in Fig. 5. Numbers refer to the neuromimes at whose output curves were obtained

the slopes are steeper. We must, therefore, amend our previous conclusion: the slope of the intensity-output curve decreases, that is, the dynamic range of the fiber decreases, as the number of sidebranches and the amount of space covered by the fiber increase.

In view of the possible implications that these experiments may have for the theory of loudness recruitment (see discussion), a series of experiments was carried out in which the analog spiral nerve was deprived of active sidebranches by removing inputs from arbitrarily chosen branches. In effect, this produces a fiber with less branches, and we should expect the slope of the input-output function to become steeper. The data wholly support this expectation; results of these "random" truncation experiments are practically indistinguishable from those obtained with "progressive" truncation as exemplified by Figs. 7, 8, and 9.

Again, because of possible implications, the question arose whether the voltage "ramp" resulting from the assumption that the stimulus is proportional to the displacement of the basilar membrane (less amplitude near the stapes than near the helicotrema) is really essential to obtain the results described. In other words, is it necessary that the effective thresholds of

the sidebranches are staggered, such that a new branch is brought into play with every few db rise in excitation? If it is true that the microphonic potential is the adequate stimulus for the nerves of the cochlea,

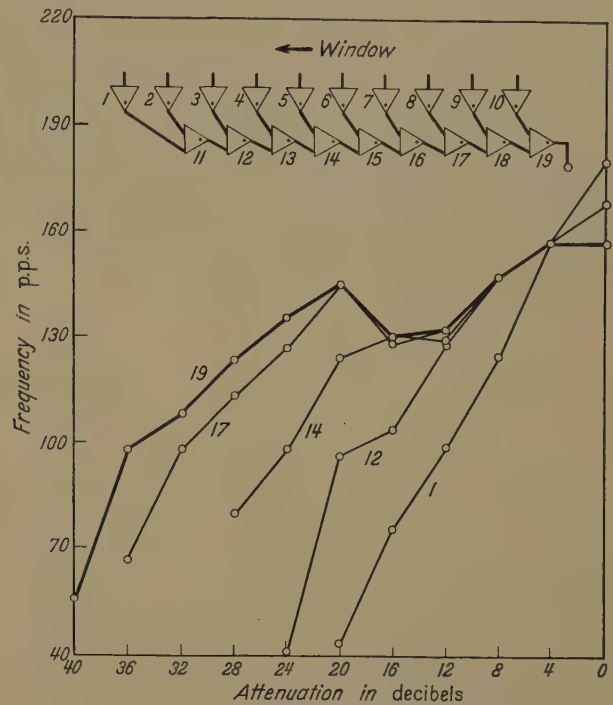


Fig. 8. As Fig. 7, but with "nerve" coursing toward base of cochlea. Same span as Figs. 5 and 7

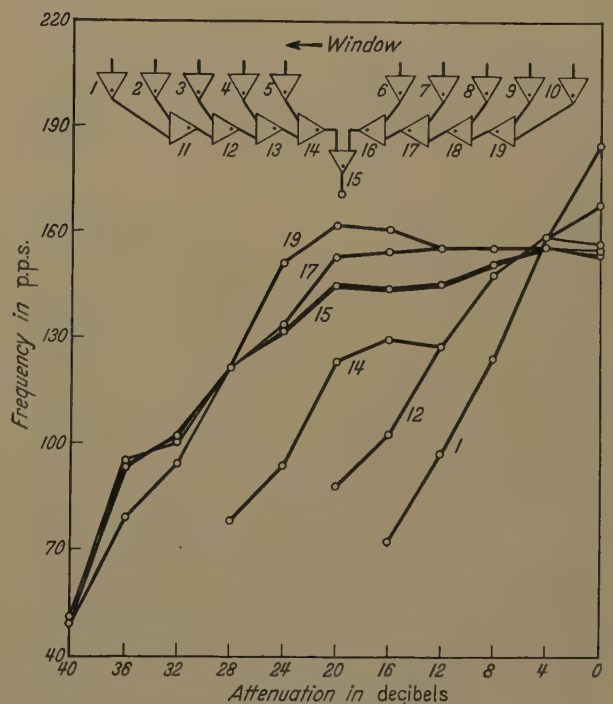


Fig. 9. As Fig. 7, but with "split" fiber

the evidence is good that in fact the stimulus does not follow the ramp-type increase, but is of about equal magnitude from one end of the cochlea to the other (TASAKI, DAVIS & LEGOUX, 1952). In experiments with neuromimes it appeared that not only is the ramp-type excitation unessential, but smoother curves are obtained with "level" stimulation (voltages at all

inputs equal), and the rule relating the steepness of slope of the input-output function with the number of branches emerges as before.

Discussion

The experiments described are based on the assumption that in some dendritic branches activity is indeed propagated in spikes, and not by some "analog" process such as electrotonic spread of excitation. There is, of course, no direct evidence that the branches of the external spiral fibers do, in fact, conduct impulses. For the contrary point of view, *viz.*, that excitation proceeds by graded potentials, no direct evidence is

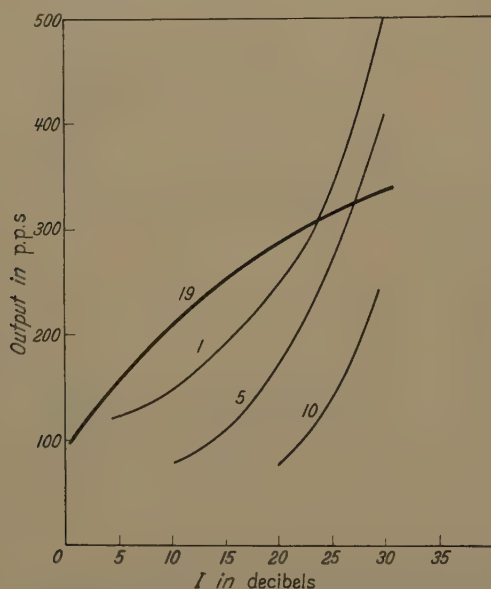


Fig. 10. Averaged curves for several experiments identical to those in Fig. 6, but with "late model" neuromimes; note that the principal difference between this and Fig. 6 is the magnitude of output frequencies

available either, although BULLOCK (1959) suggests that the dominant mode of operation of dendrites in general is by graded and continuous potentials rather than by all-or-none impulses. BULLOCK's suggestions, however, remain to be tested directly in the cochlea or other peripheral nerve endings. On the other hand, EYZAGUIRRE & KUFFLER (1955) find evidence which leads them to believe that in crayfish stretch receptor neurons, impulses may arise in the dendrites. Since no rational choice can be made at this time on the basis of available evidence, we must leave the question of dendritic signal propagation open and proceed on the assumptions stated until data accrue.

With this caveat in mind we may examine some of the possible implications of the experiments described in this paper. The first fact that merits contemplation in the input-output behavior exhibited by these chains of artificial neurons is the remarkable independence of that behavior from the particular parameters of the neuromimes used. Whether we used the original 1959 neuromimes or the very latest models (maximum firing rate: 250 and 600 pps, respectively; refractory time constant 4 msec and 2.7 msec; etc.), the shapes of the curves (after appropriate normalization of the coordinates) are as nearly identical as repeat experiments with the same neuromimes. Fig. 10 is an example of an experiment similar to that of Fig. 6,

but with late-model neuromimes; the intensity range covered is somewhat smaller (30 db *vs.* 45 db in Fig. 6), so only the initial portion of Fig. 6 should be used for comparison. It would appear, therefore, that the behavior of a spiral nerve may be rather independent of the particular properties of the dendritic segments making up the nerve.

A second fact worthy of note is the behavior of so-called "split" fibers, as exemplified by Fig. 9. When, as our usual neuromime trees are binary branching trees which have the restriction that after each decussation only one of the resulting branches can bifurcate again, the split fiber is, at least at the first bifurcation, relieved of this restriction. Nonetheless, its behavior is not different from that of the other fibers. This raises an intriguing question: is the behavior described in this paper an exclusive property of the spiral innervation of the ear, or will *any* dendritic tree behave similarly? It is easy to see that the spiral nerve, having to branch in what is practically a one-dimensional space, could not very well be built any other way. But skin nerves have no such restrictions to contend with, and their dendrites look more like the convergent arbor of Fig. 2. There are data by VON BÉKÉSY (1955) on the subjective magnitude ("loudness") of stimuli on the skin, which demonstrate that in densely innervated areas (e.g., edge of lip) the growth of sensation *vs.* intensity has a slope much more gradual than in sparsely innervated areas (e.g., cheek), where sensation magnitude rises much faster. Also, in another paper VON BÉKÉSY (1958) demonstrates that stimulation by a sharp point produces steeper slopes than stimulation by a large disk on the same skin patch. If it be true that total neuron output is proportional to sensation magnitude or loudness (see, for instance, FLETCHER, 1953), then VON BÉKÉSY's results can be interpreted on the basis of our experiments. If dense innervation is present, many sidebranches of a dendritic tree will be stimulated simultaneously by a stimulus of prescribed spatial extent. The same stimulus in a sparsely innervated area will activate fewer branches, and, in accordance with the principle proposed here, the rise in output from the latter has a steeper slope than that from the former case. The same argument holds for stimuli of different spatial extent operating on a prescribed patch of skin: a point-like stimulus activates less branches of the sensory trees than a large-area stimulus.

An additional piece of evidence bears directly on the cochlea. In 1960 BUTLER, KONISHI & FERNÁNDEZ published the finding that when the cochlea of a guinea pig is cooled below normal body temperature the steepness of the input-output function of the response increases. Since they found a corresponding decrease in microphonic potential, we might interpret their findings in the following way. As temperature decreases in the cochlea, progressively more hair cells become inactivated and incapable of generating microphonic potential. The branches of spiral nerves connecting to these inactivated cells are then effectively eliminated, and the slope of the input-output function must increase according to our model. Whether hair cells in fact "drop out" progressively (rather than decrease in output uniformly) cannot be ascertained from the results of BUTLER *et al.* Because of this uncertainty, their results on the slope of the N_1 input

output function cannot be construed as direct proof of our hypothesis, but they are at least suggestive of its validity.

This brings up a final bit of speculation: if the cochlea is damaged by trauma or pathological processes, such that some of the hair cells are destroyed and, consequently, the spiral nerve branches innervating them become inoperative, the innervation density of the cochlea is effectively decreased, while the stimulus-extent (determined solely by the mechanical properties of the cochlear partition) remains the same. We would then expect steeper slopes in the input-output relationship, as exemplified by Fig. 8. This phenomenon is known in the otological literature as "loudness recruitment"; in cases of so-called peripheral nerve-deafness, a threshold shift associated with a steep rise in the loudness curve and diminished dynamic range is observed. Typical curves resemble those of Fig. 8 remarkably well. Loudness recruitment has been definitely associated with pathological changes in the cochlear end-organs such as occur in MENIÈRE'S disease (labyrinthine hydrops) (HALLPIKE and HOOD, 1959). Present-day theories attempting to explain loudness recruitment generally follow WEVER'S suggestion (1949), that the phenomenon is due to the limitation of a limited number of receptors which normally respond to stimuli of near-threshold intensity. HALLPIKE & HOOD reject this notion on the basis of the fact that the histopathological changes extend along the whole length of the organ of Corti in MENIÈRE'S disease. Also, the "dual excitation" theory of DAVIS (1950) suggesting that the lower reaches of the loudness curve are due to the outer hair cells, while the upper part is due to the (presumably less sensitive) inner hair cells, cannot explain loudness recruitment, because HALLPIKE and HOOD find no preferential destruction of outer hair cells and preservation of inner hair cells in their cases of MENIÈRE'S disease.

Another difficulty arises in the explanation of the fact that in late chronic cases of MENIÈRE'S disease recruitment diminishes and sometimes disappears altogether while the hearing loss (threshold shift) remains (HALLPIKE & HOOD, 1959; KOS, 1955). Also, if hair cell damage persists, and no regeneration seems to take place. With the prevalent theories this fact is very hard to account for, but with the spiral nerve hypothesis the explanation is relatively straightforward. We need merely assume that a spiral dendrite will degenerate altogether when a certain critical proportion of the hair cells it innervates has been destroyed. (That nerve degeneration follows extensive hair cell damage is well known; see, for instance, WEVER 1949.) Once a whole nerve fiber with all its branches is dead, the case reduces to that of eighth

nerve interruption (as with tumors), for which loudness recruitment is known to be absent. Any residual loudness recruitment in late chronic patients can be ascribed to nerves for which the critical proportion of damaged hair cells has not been reached. The spiral nerve hypothesis thus appears to explain the main facts known about loudness recruitment. In addition it suggests a relation of auditory sensations with several other modalities, such as skin sensitivity and brightness perception in the eye. It is even possible, perhaps, to view the different subjective magnitude curves that have been obtained for many sense modalities by STEVENS (1960) and the power functions by which they can be defined, as descriptions of the innervation densities subserving those sense modalities.

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Studies with Artificial Neurons, III: Mechanisms of Flicker-Fusion

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With 15 Figures in the Text

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Summary. 1. A simple model is described which establishes a relationship between physiological and psychophysical flicker-fusion data. The three components of the model are a transducer, a filter and a flicker-detector. The model is consistent with the view that fusion is purely retinal.

2. An electronic analog is used to realize the model. Its essential elements are a source of generator potential, a low-pass filter, and a simulated ganglion cell.

3. The model was originally designed to reproduce the psychophysical results obtained by DE LANGE. Special

importance is attached to the envelope of his curves; the model reproduces this envelope. His low-intensity results are duplicated accurately, while the high-intensity, high-frequency data are derived somewhat less accurately. The high-intensity low-frequency data are attributed to a mechanism not included in the model.

4. In the simulation of physiological data obtained by ENROTH, close resemblance to the firing characteristics of retinal ganglia in cat is shown by the model. Firing occurs for bursts lasting for at most half the period of the alternating stimulus, the number of spikes per burst diminishing to unity as "fusion" is approached.

5. The phase lags and latencies of responses in the model satisfy neurophysiological evidence. Both off-latency and inhibition-latency are satisfactorily reproduced.

6. The model has been used to simulate two-component flicker data. The "flicker-detector" employed leads to results very similar to those obtained psychophysically. The phase characteristics of the assumed filter agree less well.

Introduction

There exists no model of adequate generality for the apparently simple phenomenon of flicker-fusion. The inability of the human visual system to follow the changes in intensity of a flickering light has been voluminously documented for over 200 years. Yet, as LANDIS (1953) said in his monumental bibliography, "Even such a simple point as whether the flicker-fusion threshold is dependent on retinal functional limitations or on limitations imposed by the central nervous system has never been clearly answered."

We shall describe a model of the flicker-fusion mechanism which is in close agreement with both physiological and psychophysical evidence. It is a "single element" model, i.e., one in which interactions between neighboring retinal elements are ignored. A selection of particularly comprehensive data as the basis for the design of the model justifies its presentation in a field where so many already exist (IVES, 1922b; HECHT & VERRIJP, 1933; DE LANGE, 1952; KELLY, 1960; DE LANGE, 1961).

Although we make no attempt to resolve the question of peripheral *vs* central fusion, (the model is consistent with either point of view), some bias for retinal fusion will be apparent. The model has been designed to show readily the correspondence between its components and retinal components. It is consistent with physiological evidence which implies the possibility of purely retinal fusion (GRANIT & THERMAN, 1935; HARTLINE, 1938; ENROTH, 1952; SVAETICHIN, 1956).

Purely analytical or mathematical models are not readily applicable to complex, nonlinear systems (e.g., neural structures). The detailed behavior of such abstractions may be difficult to predict. Furthermore, unwelcome constraints and simplifications often become necessary. In such cases a physical model which can be used to yield experimental data is often useful. Employed literally as an analog computer, a physical model can be instructive, readily manipulated and stimulating.

We have built an electrical circuit for this purpose and have investigated the correspondence between components of the circuit and some of those in the physiological system. Various signals which appear at different places in the model's "visual pathway" have been compared with signals in the physiological visual pathway to test the relevance of the model. The output response of the circuit is similar to that of a

retinal ganglion cell; this has been accomplished by using an electronic analog of a generalized neuron (HARMON, 1961).

The design criteria for a model of flicker-fusion are not easily stated. There has been no apparent common basis on which to evaluate psychophysical data derived from the great variety of classical stimulus presentations such as rectangular waves of varying light-dark ratio, triangular waves, repeated brief flashes and the like (e.g., IVES, 1922a; ROSS, 1938; BROWN & FORSYTH, 1959; BARTLEY & NELSON, 1961). However, in recent years flicker-fusion has been investigated by new and revealing techniques. Particularly important studies are those by DE LANGE (1952, 1954, 1958), and by ENROTH (1952). The new information, no less significant than Talbot's law or the Ferry-Porter law, has received less attention in the literature than it deserves.

DE LANGE's results show that in the human visual system, response is rapidly attenuated with rising frequency for sine waves above 10 c/s. Therefore, for these frequencies the fundamental component of *any* stimulus waveform is the most significant; higher harmonic components are progressively less effective. By considering the stimulus as a composite of sinusoidal components and by taking into account the attenuation observed by DE LANGE, a unified understanding of much of the previous work is made possible (DE LANGE, 1958; LEVINSON, 1959; KELLY, 1961). We thus feel justified in considering DE LANGE's research as representative of a large body of flicker-fusion psychophysics. Consequently our model has been designed to reproduce the most significant aspects of DE LANGE's data.

Bearing closely on DE LANGE's psychophysical results are the physiological findings of ENROTH, although the connection may not be immediately obvious. ENROTH's work supplies data on the latencies of cat retinal ganglion responses to flicker. These data complement the attenuation properties mentioned above. Understanding the relationship between latency and attenuation is critically important because no explanation of the fusion mechanism which includes one and ignores the other is complete. The model to be described accounts for both the observed latencies and the attenuation characteristics by a relatively simple system in which each property implies the other.

An examination of the characteristics of the model which were required by physiological considerations led to the prediction of new psychophysical results. This prediction was then used to test the validity of the model.

Psychophysical considerations

DE LANGE's advance followed from the realization that the light stimulus must be controlled for two parameters, average (steady-state) and alternating illumination. In traditional flicker presentations the amplitudes of the average and alternating components of the stimulus vary at once and are not separately controlled, e.g., where the light-dark ratio is used as a parameter. Since it is well known that changes in average illumination modify the eye's adaptation, the absence of proper control over the stimulus was a serious shortcoming. DE LANGE's flicker stimulus was

obtained by sinusoidal modulation of an otherwise steady light. Since both the average illumination and the depth of modulation were separately variable, he had independent control of the two stimulus components. The presentations were foveal, and the luminances were in the photopic range.

Fig. 1 shows some typical results replotted from DE LANGE (1958). We retain DE LANGE's convention of plotting the ordinates with increasing intensity downwards so as to reveal the resemblance of the curves to attenuation characteristics of electronic systems. The curves plot the peak amplitude of the sinusoidal modulation as a function of its frequency at fusion threshold. Each curve represents a different average retinal illuminance I on which the alternating component i_0 was superimposed. Above 10 c/s, i_0 must be increased to achieve higher fusion frequencies.

DE LANGE customarily plotted not the absolute modulation amplitude (as shown here) but its percentage of the average illuminance. We have replotted his results in order to reveal the fact that all the curves have a common envelope, as indicated by the dashes.

We attach considerable importance to this envelope. Its equation is simple, having the form of the well known Ferry-Porter law which relates fusion frequency to illuminance,

$$f = A \log i_0 + B.$$

The envelope sets a bound upon the amplitude-frequency range within which flicker may be observed, regardless of average illuminance. This suggests the existence of a specific visual mechanism of limited high-frequency response. This mechanism is simulated in our model by a low-pass filter.

The additional loss of flicker sensitivity represented by the dips in the high-intensity curves at low frequencies is a function of average illuminance I . We feel that this should be attributed to the action of an additional mechanism, one not included in the present model¹. The requirement for some other mechanism is also suggested by the common subjective experience that the setting of flicker-fusion threshold is a different task at low and at high frequencies. This subjective impression is reinforced by the findings of KELLY (1959) that modulation amplitudes for fusion at low frequencies depend markedly upon the nature of the surround of the test spot, but that at high frequencies the surround has relatively little influence. Thus, while a single-element model may account for all the high-frequency data, it cannot lead to *all* the low-frequency data. To this extent then the present model represents a compromise. It will be seen to account adequately for the envelope of DE LANGE's results and for the two low-intensity curves as well.

Thus far we have considered the attenuation-with-frequency characteristics of the visual system, observing with DE LANGE that such characteristics are produced by a low-pass filter. We still require a sensing element after the filter. It seems reasonable to assume that this element reacts only to a change in filter output, regardless of filter input. That is, we postulate that there is a particular site in the visual system where there is constant physiological response

at fusion threshold. The requisite sensing element following the filter would be a nonlinear threshold mechanism. This is a "flicker-detector", its functional analog providing another component of the model. The physiological evidence for flicker detection by retinal ganglion cells is described in the following section.

Physiological Considerations

ENROTH (1952) recorded spikes at the retinal ganglia of cats and demonstrated the relationships

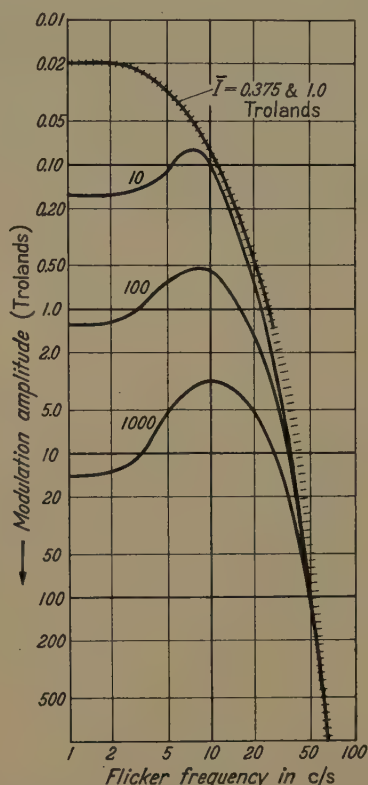


Fig. 1. "Flicker attenuation characteristics" (DE LANGE, 1958). Intensity of light modulation as a function of critical flicker frequency at constant average illuminance, I . Ordinates represent the peak amplitude i_0 of the sinusoidal modulation required for fusion threshold. Dashes indicate envelope to all curves

between flicker frequency and bursts of spikes in single cells. Fig. 2 reproduces one of ENROTH's recordings.

Light is recorded in the upper traces, *on* and *off* respectively being represented by upward and downward displacements. Neural action potentials are shown in the lower traces. The ganglion cell from which the recording is taken is of the *off* responding type; a burst of spikes occurs in response to each cessation of illumination. The number of spikes in each burst diminishes roughly monotonically as the stimulus frequency is increased. The duration of spike burst is always less than half the period of the repetitive stimulus.

The latency between light *off* and neural response appears to be approximately constant with frequency. Note, however, that at the point that the ganglion firing fails to be synchronous with the stimulus (arrow in figure), the latency of response extends over more than one complete stimulus cycle. Delays of this magnitude are usually concomitants of steep slopes in the attenuation characteristics of simple (linear) filter systems. Thus these physiological data also

¹ Such a mechanism might operate by frequency- and intensity-dependent feedback. The sort of feedback provided by lateral inhibition or efferent innervation could account for such action.

support the hypothesis of a low-pass filter which was implied by psychophysical findings. Obviously, more complex (nonlinear) filters can be conceived which produce similar results. The linear low-pass filter seems to be the simplest one which satisfies our requirements; parsimony inclines us to explore its implications before investigating more complicated filters.

Other evidence for retinal filtering has been obtained from the ommatidium of *Limulus* (HARTLINE,

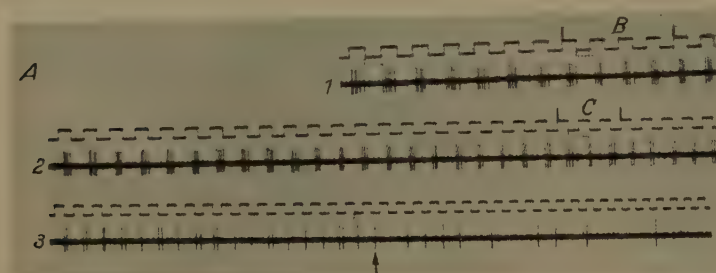


Fig. 2. Response of cat retinal ganglion cell to flickering light (ENROTH, 1952). Top lines—square-wave light stimulus of increasing frequency. Bottom lines—spike output recorded in ganglion cell. Unit is of the off responding type; off-latencies are indicated by dotted lines. "Fusion" is said to occur at arrow, line 3, where synchronized response fails

H. K., MILLER, W. H. & RATLIFF, F., personal communication). For a square-wave light stimulus at very low frequencies, a "slow potential" is observed which has approximately the waveform of the stimulus. However, for stimulus frequencies above about 5 c/s the slow potential becomes sinusoidal. Similar action has been noted by SVAETICHIN (1956) in the retina of sunfish (*Lepomis spp.*).

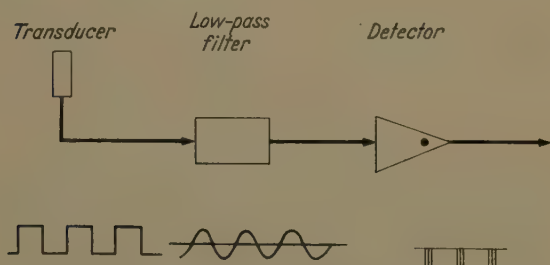


Fig. 3. Functional representation of three-component model. Transducer converts square-wave light stimulus into square-wave physiological signal; low-pass filter converts square waves into sinusoids; detector sets fusion threshold and responds with spike output to filtered signal

ENROTH's criterion for fusion is based on the termination of synchronized response. Fusion is said to occur at that stimulus frequency for which the number of ganglion spikes per burst diminishes to unity and beyond which erratic or no firing is observed (arrow in Fig. 2). The ganglion cell thus appears to play the role of flicker-detector. This is the threshold device mentioned above which was postulated to follow the filter mechanism.

The Model

Fig. 3 shows the "single element" model. It has three components. First, a transducer accepts a light signal and produces a signal of some other nature. A filter which possesses the frequency dependence observed by DE LANGE follows. Finally, a threshold device (detector) operates with the firing characteristics found by ENROTH.

The physical realization of this model incorporates the attenuation with frequency, the latency, and the ganglion-cell firing characteristics which have been described. A transducer was not included for the reason that it is not functionally important for this model whether the initial transduction in the photoreceptor is chemical, ionic or electronic. It is sufficient to represent it by an arbitrary parameter which ultimately produces the equivalent slow potential. Consequently an electrical voltage is used to represent the light input. It is applied directly to the low-pass filter.

The filter is linear; phase and attenuation are related simply (see Appendix). It possesses attenuation and delay characteristics such that its output is sinusoidal over most of the frequency range of interest, irrespective of whether the input waveform is sinusoidal, square, triangular or the like. Five independent resistance-capacitance low-pass filter stages are used. The attenuation rate thus approaches 1.5 log units per octave—an intermediate value which leads to the best over-all fit to DE LANGE's data. The filter

cutoff frequency is 10 c/s. The delays introduced by this filter are of the required magnitudes, as will be discussed below.

The flicker-detector is represented by an electronic analog of a neuron ("neuromime") of the type described by HARMON (1961). To satisfy ENROTH's results it must be arranged to produce a burst of spikes for each half cycle of the stimulus, the number of spikes per burst diminishing with decreasing excitation. Furthermore, as may be seen in Fig. 2, the latency per stimulus cycle must increase with frequency, and the latency from stimulus off to response must be less than that from stimulus on to termination of response.

Like the natural neuron, the neuromime responds only to unidirectional (cathodal) stimulus and fires only if its threshold is exceeded. Hence for a sinusoidally shaped stimulus whose average value is zero, the neuromime behaves as a half-wave rectifier. Since in practice its threshold is not exactly zero, but is arbitrarily set by its internal circuitry¹, excitation typically occurs during less than half of each cycle.

Excitation time and duration depend upon the amplitude of the sinusoid developed by the filter. As a stimulus is increased in frequency or decreased in amplitude, the excitation available to the neuromime is both briefer and less intense. In a typical flicker experiment, stimulus amplitude is held constant as frequency is increased. This is reflected in the neuromime's firing as schematized in Fig. 4.

Three cases are shown. At an input frequency of 10 c/s, the filter develops a relatively large-amplitude sinusoid which considerably exceeds threshold and which evokes a burst of spikes from the neuromime. The delay, indicated by the dashed line between square wave and sinusoid, is somewhat longer than half the stimulus period.

If the up-going direction is taken as on for the stimulus, then the response illustrated may be arbit-

¹ The results would have been very little affected by using some other threshold value.

y taken for the *off* half cycles to correspond with results shown in Fig. 2.

At 15 c/s the same input amplitude produces an attenuated filter output which is manifested in the neuromime's output by fewer spikes per burst, decreased duration of burst and increased relative latency. The absolute value of latency is little changed; however, at this increased frequency it now represents only one full period of delay relative to the stimulus.) Finally, at 25 c/s the excitation available to the neuromime just reaches threshold, evoking one spike per a delay of approximately one stimulus cycle. At beyond this point firing may be erratic (because of noise in the system). At higher frequencies, given the same stimulus input amplitude, threshold is not reached, and no firing occurs. Given a larger stimulus amplitude, firing could be evoked beyond 25 c/s.

The latencies in this model are made up of two independent components, the filter delay being the larger one. An analysis of this action and circuit details of the model appear in the Appendix.

Experimental Results

1. Simulation of psychophysical data. The envelope of the flicker-fusion "attenuation characteristics" of DE LANGE is easily duplicated. A sinusoidal stimulus was employed in order to be consistent with DE LANGE's procedure, although square waves would have yielded identical results owing to the action of the filter (except at very low frequencies).

In order to obtain the required characteristics, attempts of "fusion" must be established. To do this we adopted ENROTH's fusion criterion. For constant stimulus amplitude, frequency was increased until the number of neuromime spikes per burst diminished to unity and synchronous firing ceased. At this point fusion was declared and the frequency noted. These results are shown in Fig. 5, superimposed upon the DE LANGE curves which appeared in Fig. 1.

The dots represent measured points. The psychophysical data cover a wider stimulus range than we were able to employ with the model because of the difficulty of obtaining and handling the required alternating voltage (a range of 50,000:1).

We may extrapolate our results analytically according to the equation

$$E = 0.0177 [1 + (f/10)^2]^{5/2}$$

where E is the peak amplitude of the input voltage at the fusion frequency f . This expression applies to a 5-stage filter (see Appendix) with parameters determined from our experimental data. Circles in the figure represent the extrapolated points.

It will be seen that the model's characteristic curve follows the low-intensity data and is roughly the envelope of the rest of DE LANGE's results. The model to the low-intensity data would be better with a lower cutoff frequency of 11.3 c/s instead of 10.0 c/s, though to the high-intensity data it would be worse.

2. Simulation of physiological data. The latency and firing characteristics required by ENROTH's findings are accurately reproduced by the model. Typical responses are illustrated in Fig. 6. Input square-wave amplitude was held constant while the frequency was varied from 10 c/s to slightly over 25 c/s. The number of output spikes per burst diminishes monotonically

with increasing frequency until at 21 c/s there is one spike for each *off* stimulus. This continues until at 24.5 c/s occasional spikes drop out. At 25.5 c/s only a few spikes are observed. By 26 c/s there is no further output; the excitation available from the filter lies

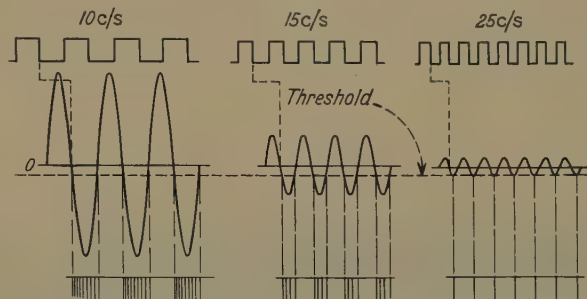


Fig. 4. Schematic attenuation and phase lag action of filter and consequent neuromime response. As input amplitude is held constant and frequency is increased, available excitation to neuromime is diminished. Latency (short dashes) increases on a per cycle basis. Spike production occurs during time that excitation exceeds threshold. Spikes per burst diminish in number as excitation decreases

well below the neuromime's threshold from this point on. Note the similarities to the physiological results of Fig. 2.

ENROTH describes two parameters of latency. For the *off* receptors under consideration, the "off-

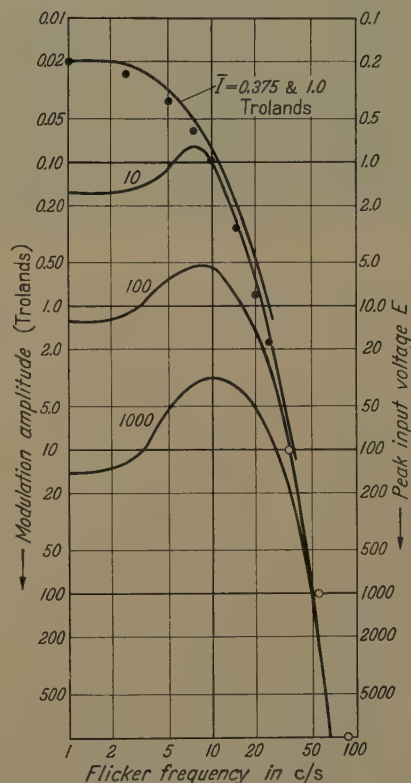


Fig. 5. Flicker attenuation characteristics of Fig. 1 with data from model superimposed. Dots—measured values; circles—extrapolated values

latency" is defined as the interval between the stimulus turn-off and the initiation of a ganglion cell output burst. "Inhibition-latency" is defined as the interval between the subsequent turn-on of the stimulus and the termination of the burst. The curves of Fig. 7 represent theoretical off-latency (A) and inhibition-latency (B) for the model (see Appendix for derivation).

The points associated with each curve are measured responses of the model. Off-latency can be measured directly, of course, by noting the time at which firing begins. It is not possible to verify the theoretical inhibition-latency precisely since the last spike in a burst is not necessarily coincident with the threshold crossing of the sinusoidal excitation. Consequently, the points corresponding to inhibition-latency (circles) are approximations obtained by extrapolation.

The action of a circuit used to obtain adaptation (see Appendix) introduces additional discrepancy between measured and theoretical inhibition-latencies.

system for threshold flicker. If the visual system has a "flicker-detector" as postulated, then we might also expect it to respond differently to different waveform forms. Such waveform sensitivity, if found psychophysically, would be of use in further validating the model.

To test for waveform sensitivity one cannot simply modulate the light with a wide variety of complex waveforms. The frequency dependence of the visual system insures that the higher harmonic components of the stimulus (which generate the complexity of the waveforms) are severely attenuated. Thus, in terms

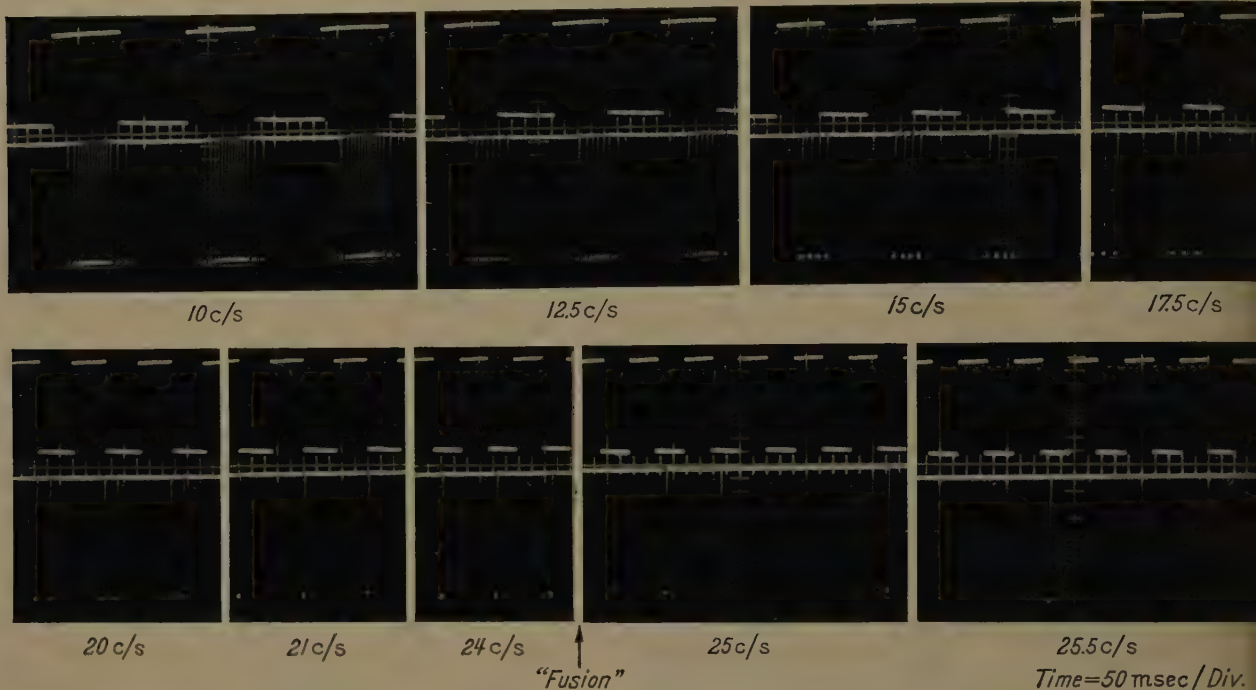


Fig. 6. Square-wave stimulus, and neuromime response as a function of frequency at constant amplitude. Compare with physiological results Fig. 2. Spikes occur in regular bursts for each half cycle of stimulus, decreasing in number per burst as frequency is increased. Regular firing ceases past 24.5 c/s. After 26 c/s no further output could be obtained

This circuit deforms the half-sine wave into a shape which provides a fast rising and slowly decaying voltage. The resultant firing frequency has a high initial rate and then slowly diminishes.

The shapes of the curves of Fig. 7 are similar to some of those given by ENROTH. The variability among the units she tested, however, does not allow extremely close comparisons to be made. Note, however, that at *any* frequency the inhibition-latency is shorter than the off-latency, in accord with the physiological data; i.e., firing always occurs for less than a half cycle. ENROTH points out that at fusion (off-latency)—(inhibition latency) = flash duration = dark period. The "fusion" frequency in the model experiment described above was about 24.5 c/s. From Fig. 7 it is seen that at this frequency the off-latency is approximately 47.5 msec, and the inhibition-latency is about 28 msec. The difference of 19.5 msec corresponds closely to the half period (flash duration) of 20.4 msec.

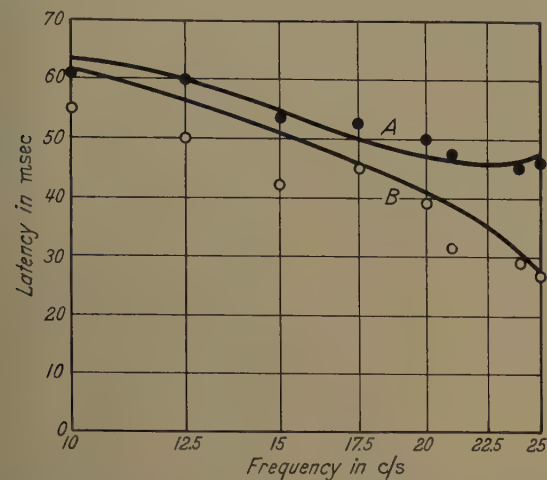
3. *A test of the model.* Consideration of our theoretical model suggested a new technique for psychophysical investigation of flicker-fusion. Thus far, we have confined our attention to simulation of the amplitude and the delay characteristics of the visual

of our model, most waveforms are reduced to the fundamental sinusoid by the time they reach the flicker-detector. Consequently, in order to investigate waveform sensitivity at the detector, appropriate stimulus compensation must be supplied. Details of the method have been described by LEVINSON (1960).

Briefly, the procedure consists of modulating stimulus light by a waveform which is the sum of two sinusoids, a fundamental and its second harmonic. Compensation is achieved by allowing a subject to see the amplitude of each component separately to fusion threshold. Thus, the two stimulus components produce equal "sensation levels". However, the stimulus amplitudes are generally quite different. For example, at frequencies of 10 and 20 c/s, the fundamental stimulus amplitude is only one-tenth that of the harmonic.

When the light is modulated by the sum of the two adjusted components, flicker is again apparent. The reason for this is that the peak amplitude of the combined waveform is greater than that of either component. This may be seen by referring to Fig. 8. The fundamental and the second harmonic are shown with equal amplitudes to represent the presumed condition at the flicker-detector. Their combined

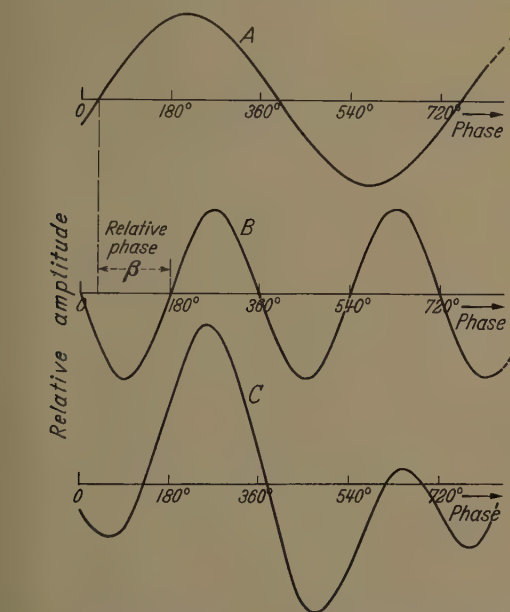
veform is shown in the lower trace. It varies with the relative phase β , as defined in the figure. β is not exactly measurable, of course, but will differ by some constant amount from the relative phase α between



7. Delay as a function of frequency. A—"Off-latency", the interval between stimulus turn-off and initiation of response. B—"Inhibition-latency", the interval between stimulus turn-on and cessation of response. Curves are theoretical; points show measured values

the stimulus components. The constant difference between α and β is contributed by the filter.

Since the combined-modulation amplitude exceeds the threshold of the flicker-detector, a reduction in stimulus amplitude is required to re-establish fusion.



8. Two-component waveform (C) derived from fundamental (A) and a second harmonic (B). The form shown is the sum of A and B for the indicated relative phase, β , between A and B. Phase is given in degrees of the 2nd harmonic cycle

Further, the reduction required will vary with β . This dependence may be understood from Fig. 9.

All four waveforms result from combining two equal-amplitude sinusoids which differ in frequency by a factor of two. Each waveform arises from a different value of β , as indicated. These quite dissimilar waveforms result from stimulus waveforms which differ very little since the light modulation is predominantly second harmonic (due to the low amplitude of fundamental which is required). However, it is just the

small contribution of the fundamental which so markedly modifies the waveform at the detector.

A detector might discriminate between these waveforms on the basis of any one or more of several parameters. For example, the 0° and 180° waveforms have the greatest total excursion (peak-to-peak values) while the 90° and 270° waveforms have the greatest positive and negative (peak) excursions, respectively.

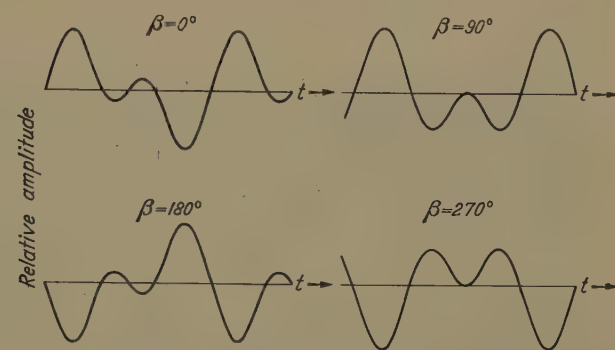


Fig. 9. Two-component waveforms for four particularly significant values of relative phase

A peak-to-peak detector would exhibit maximum sensitivity to either member of the first pair. A peak detector would be most sensitive to one or the other of the second pair (but not to both), depending on its preferred polarity. Thus, a peak-to-peak detector would exhibit two maxima in each 360° , while a peak detector would show only one.

The results of the psychophysical experiment performed to test for waveform sensitivity are given in the upper trace (A) of Fig. 10. The required fractional reduction of amplitude is plotted as a function of relative phase α . The frequencies employed were 10 and 20 c/s. Averaged data for five observers are shown.

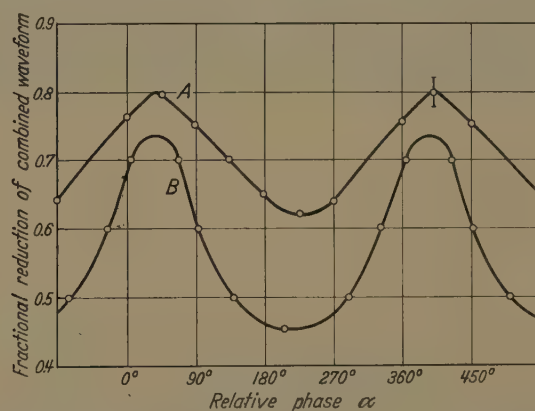


Fig. 10. Flicker sensitivity as a function of waveform. Two sinusoidal modulations, 10 and 20 c/s, are individually set to fusion threshold. When these two components are combined, their amplitudes must be reduced to re-establish fusion threshold. Ordinate values represent the required proportional reduction as a function of the relative phase α between the sinusoids. A—Psychophysical results averaged over five subjects. B—Data obtained from electronic model

It is clear that phase sensitivity exists. Further, since the sensitivity maxima (dips in curve) occur every 360° and not every 180° , the detector behaves like a peak detector.

This experiment was duplicated with the electronic model. Frequencies of 10 and 20 c/s were again employed. The voltage at each frequency was independently set to fusion threshold as previously defined.

The two voltages were then added at various relative phases. As in the psychophysical experiment, this brought response above fusion threshold. The amplitude of the combined waveform was reduced until fusion threshold was re-established. The fractional reduction is plotted in curve B.

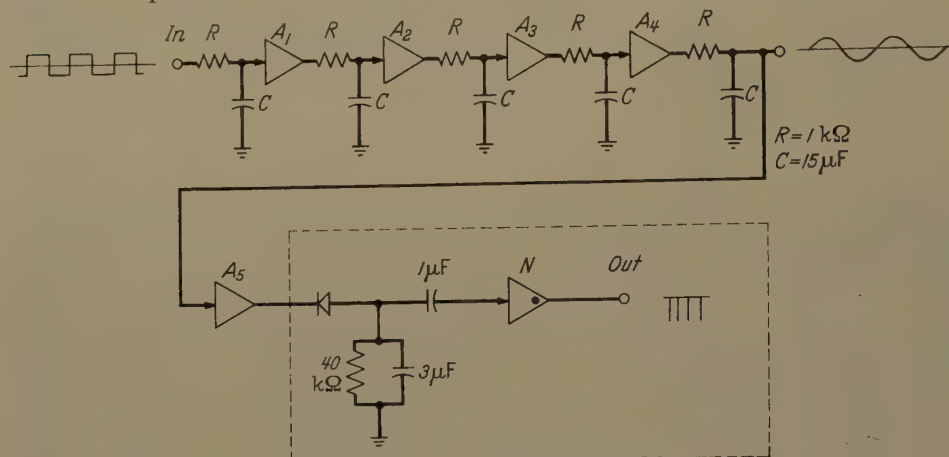


Fig. 11. Schematic of electronic model. Square-wave voltage stimulus, applied to five independent low-pass filter stages, emerges as a sinusoidal voltage. The filter stages are isolated by unity-gain amplifiers (A_1 — A_5). After final amplification (A_6) the signal is shaped and introduced as an excitatory voltage to a simulated neuron (N). The final response is a series of spikes

The most significant similarity between the two curves is that each exhibits only one sensitivity maximum in 360° of relative phase. The qualitatively good agreement of the two curves provides further evidence for the appropriateness of the model.

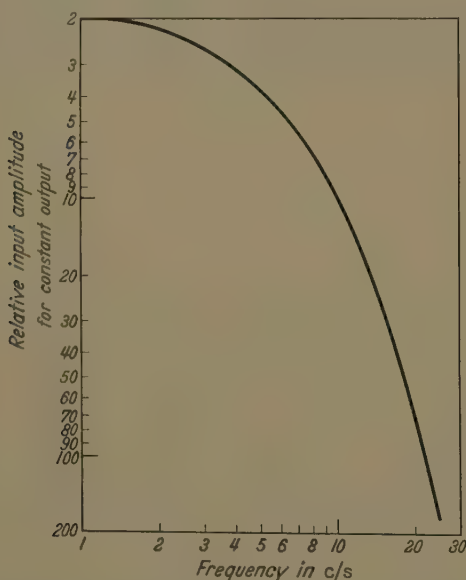


Fig. 12. Filter attenuation characteristic. The five independent stages of the low-pass filter have a combined cutoff frequency of 10 c/s. Response falls off rapidly with increasing frequency, approaching 1.5 log units/octave. Response is indicated by plotting downward the increasing input amplitude required for constant output

It is difficult to set a criterion for quantitative agreement. The ordinates of the two curves agree only approximately. Also, the precise phase matching of maxima and minima is accidental; further consideration showed that such precision is hardly to be expected. This point is discussed below.

Discussion

With reference to ENROTH's criterion for fusion, it should not necessarily be inferred that the animal's

fusion threshold lies at that frequency at which all ganglia cease firing synchronously. It seems more reasonable to assume that flicker appears to fuse when some percentage of ganglia cease to follow. Inasmuch as ENROTH demonstrated a wide spread in the distribution of thresholds among a population of ganglion cells, we assume that a psychophysical fusion threshold some ganglia will still be firing several spikes per half cycle some will be in ENROTH's fusion condition, and some will no longer be following the stimulus at all. The "fusion" data derived from our model represent those cells in ENROTH's fusion condition.

If the information produced by the ganglia is transmitted as such, then the only role to be played by more central mechanisms is the setting of a fusion criterion on the basis of the percentage of ganglia still firing. Variations in this criterion may occur but are not of interest at the moment.

Looking at fusion in this light resolves the apparent conflict arising from evidence that ERG and cortical responses to flicker may be present even though the subject reports fusion (VAN DER TWEEL, L. H., personal communication; LINDSLEY, 1960).

In the initial stages of developing our model we considered only the filter characteristics required to fit DE LANGE's results. It was subsequently noted that the delays inherent in the proposed filter were of the order of magnitude of the ganglion response latencies found by ENROTH. By applying her physiologically derived definition of fusion to a generalized model of a neuron, the physiological and the psychophysical requirements were satisfied simultaneously.

These points taken together strengthen the hypothesis that fusion is established retinally. To test this hypothesis further, additional physiological evidence is required. Measurements of attenuation and delay under steady-state flicker stimulation at various points in the same visual system would be most helpful. The low-pass filter action which has been observed could arise from a number of mechanisms which act slowly and cannot follow high frequencies, e.g., photochemical reactions, ion diffusion and depletion systems, and synaptic and dendritic conduction processes. Precise knowledge of both attenuation and delay is required in order to discriminate between different possible models of the fusion mechanism.

The rectifying property of the neuron (included as a general function prior to these experiments, but required also by ENROTH's data) was found to be essential for deriving the two-component flicker results. We have noted that the two-component flicker data obtained from the model were only qualitatively similar to those obtained psychophysically. Two important discrepancies should be noted. First, the response of the model was sharper. Second, it was

tioned that the precise positional matching of response peaks was accidental. This became apparent in further psychophysical experiments were conducted using frequencies different from those reported.

The results for 20 and 40 c/s revealed a sensitivity peak at about 65° . For the model this peak would appear at 165° .

Thus the two-component flicker method provides a critical test of the model. It lends qualitative support, but discloses a quantitative inaccuracy in the characteristics. Note that the error of 100° at 40 c/s corresponds to less than 7 msec. error in latency, the total latency in the system is on the order of 50 msec. This small discrepancy would be reduced in a model having delay independent of frequency. It is difficult to conceive of a single-element receptor system in which attenuation depends on frequency but delay does not. Summation from an ensemble of retinal elements having an appropriate distribution of delays could produce such response. It is well established with few exceptions there is not a one-to-one anatomical or physiological communication between photoreceptor and ganglion cell. A parallel filter, representing a number of laterally interconnected retinal units, is presently being investigated.

Appendix

Circuit details of the model. The circuit from which all experimental results were obtained is shown in Fig. 11. Input signals are filtered by five independent RC stages. Each stage is isolated by a unity-gain amplifier (A_1 to A_4). The measured cutoff frequency f_0 of the complete filter is 10.0 c/s.

The measured attenuation-frequency characteristic is given in Fig. 12.

Note that this curve is reflected in the "fusion" data derived from neuromime as plotted in the points of Fig. 5. Delay characteristics of the circuit will be discussed below.

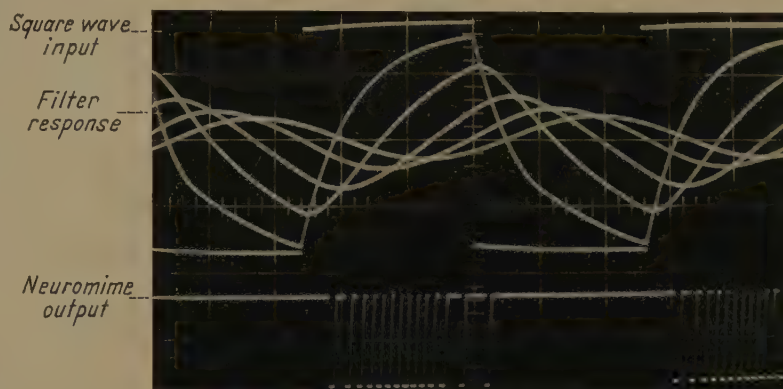
The output of the final amplifier (A_5 in Fig. 11) provides the excitation for the ganglion cell analog (see enclosed enclosure). The purpose of the diode and the network to ground is to provide an input waveform to the neuromime which produces a rate of firing that is off, i.e., adaptation. (This is an alternative method to that described by HARMON, 1961). This circuit provides some additional filtering, but its principal function is to distort the sine waveform. There is negligible effect on the critical flicker frequency as is evidenced by the above noted agreement between the measured attenuation characteristic (Fig. 12) and the fusion data (Fig. 5). The introduction of this circuit is the average value of the excitation from its initial value of zero volts; the capacitive input (10 μ F) to the neuromime restores the zero average.

The composite nature of delay. It will be convenient to consider delayed response both in terms of phase lag and of latency. By phase lag we mean the

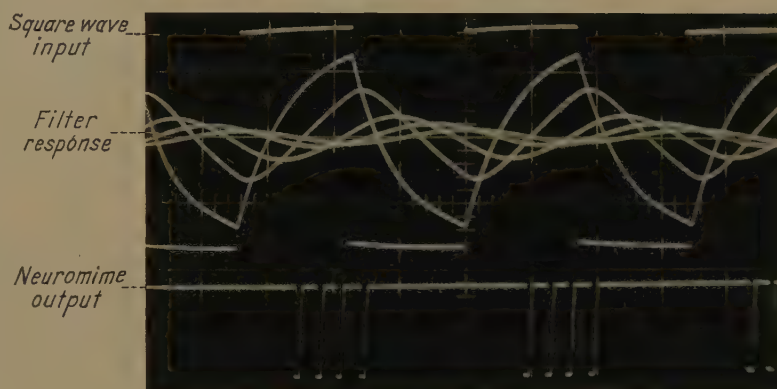
number of degrees delay per cycle. By latency we mean the corresponding delay expressed in units of time.

The total delay between stimulus and response comprises two independent components. Delay in the filter is the predominant one and is independent of input amplitude. The filter action is illustrated in Fig. 13.

The upper section of A illustrates the response for a 10 c/s square-wave input. Filter response waveforms



A. 10 c/s, 20 msec/Div.



B. 15 c/s, 20 msec/Div.

Fig. 13. A—At the top, square-wave input and responses measured at each of the five successive filter stages for 10 c/s input frequency. At the bottom, neuromime firing response to the filter output. B—Similar measurements for 15 c/s input frequency. As frequency is increased, amplitude of filter output becomes smaller, and spike frequency and number are diminished.

were taken at each of the five filter stages. As the signal progresses through the filter, its amplitude diminishes and phase lag increases until, after five stages (smallest sine wave), the attenuation is 0.75 log units, and the phase lag is almost 220° . The responsive firing of the neuromime, shown in the lower trace, occurs after a total lag of slightly over 220° . At 10 c/s this corresponds to a latency of 61 msec. The response is a burst of 14 spikes lasting for approximately 50 msec.

At 15 c/s (Fig. 13, B) attenuation and phase lag are increased. The filter output now is a fundamental-frequency sinusoid which is approximately 1.25 log units below the unfiltered amplitude and which lags by about 300° , nearly one full cycle. The neuromime response is a burst of only four spikes lasting for 21 msec, which is considerably less than half a period.

The second component of delay is present but is not readily apparent in Fig. 13. It is due to the fact that

the excitation takes some time to reach the neuromime's non-zero threshold. This may be seen by referring to Fig. 14¹. The filter phase lag, shown as Φ , is defined as the interval between stimulus *off* and the resultant zero crossing of the sinusoid. The additional lag from that point to threshold crossing is shown as Θ .

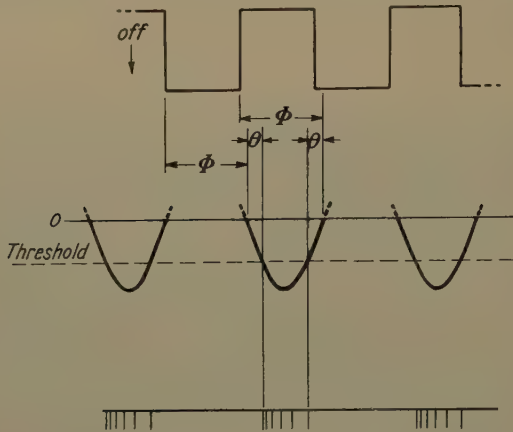


Fig. 14. Schematized representation of the composite nature of delay. Top—square-wave input. Center—sinusoidal filter output. Bottom—neuromime spike output. Filter phase lag Φ makes maximum contribution to delay. The other component Θ is due to the nonzero neuromime threshold. Off-latency is determined by $\Phi + \Theta$; inhibition-latency is determined by $\Phi - \Theta$.

Both Φ and Θ are expressed in degrees so as to put them on a *per cycle* basis. For increased stimulus amplitudes Φ will remain constant but Θ will diminish. For decreased stimulus frequency both Φ and Θ will diminish. The total phase lag from stimulus *off* to

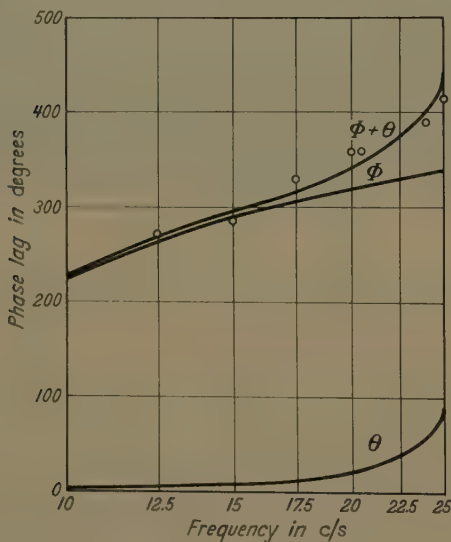


Fig. 15. Phase lag between stimulus and response is a function of two variables. Φ —Theoretical lag due to low-pass filter action. Θ —Theoretical lag due to interaction of half-sine wave with neuromime threshold. $\Phi + \Theta$ —Total phase lag. Points show measured values

neuromime firing is $\Phi + \Theta$. Similarly the interval from stimulus *on* to cessation of response is $\Phi - \Theta$.

The variations of Φ and Θ with stimulus frequency are shown in Fig. 15. The middle curve (Φ) results

¹ Distortion of the excitation waveform to obtain adaptation is ignored here for simplicity of analysis. The small effect of the distortion on delay may be seen in the experimental results (Fig. 7).

from the action of the 5-stage filter. It follows the relationship

$$\Phi = 5 \cos^{-1} [1 + (f/f_0)^2]^{-1/2}$$

where f and f_0 are the input frequency and the filter cutoff frequency respectively. The expression is the relationship holding for a filter consisting of five dependent RC stages.

The lower curve (Θ) represents the additional phase lag due to the changing amplitude of the filter output as frequency is varied. It would be zero for an infinitely large output. The delay reaches a maximum of 90° when the filter output is just equal to the neuromime's threshold. By ENROTH's definition this is the fusion condition. This value of maximum delay is consistent with ENROTH's observation that at fusion the difference between off-latency and inhibition latency is equal to the stimulus half period. Expressed as phase lag,

$$(\Phi + \Theta) - (\Phi - \Theta) = 180^\circ$$

and so

$$\Theta = 90^\circ.$$

Theoretical values of Θ may be derived from

$$\Theta = \sin^{-1} V/E$$

where E is the peak amplitude of the half sinusoid (filter output), and V is the threshold. Since the aftereffect characteristic of the filter can be expressed

$$E/E_i = [1 + (f/f_0)^2]^{-5/2},$$

(where E_i is the input amplitude to the filter), Eqs. (2) and (3) can be combined to yield

$$\Theta = \sin^{-1} [(V/E_i) [1 + (f/f_0)^2]^{5/2}].$$

This is the expression satisfied by the lower curve of Fig. 15.

The composite, total delay $\Phi + \Theta$ is plotted at the top of the figure as the sum of the other two curves. The points shown are experimental values obtained from the data in Fig. 6. These results are in reasonably good agreement with those of ENROTH, in which the phase lag varies monotonically from about 190° at 10 c/s (start of line 1, Fig. 2) to approximately 420° at the 20 c/s fusion point (arrow in line 3, Fig. 6).

The theoretical latencies discussed earlier (Fig. 7) were derived directly from the phase lags just described. For example, each value T of off-latency is obtained from

$$T = \frac{\Phi + \Theta}{360^\circ} \cdot \frac{1}{f} \text{ seconds}$$

which is simply phase lag expressed in units of time.

We are indebted to C. ENROTH, H. DE LANGE, Dzn., and D. H. KELLY for their stimulating and helpful correspondence.

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Nichtdigitale Lernmatrizen als Perzeptoren

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Mit 12 Textabbildungen

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Summary. Hitherto it was assumed that the input signals learning matrix are digital, especially binary. In this paper properties of learning matrices capable of learning and assing accordingly patterns of non-digital nature are igated. It is shown that the recognition of patterns by s of such non-digital learning matrices offers extraordinary abilities for the formation of invariants. For the deson of the learning process a formal "perceptor" is defined, properties of which are characteristic of both organic and ological perceptors. In addition, it is shown how the ological realization of non-digital learning matrices can be accomplished.

Gliederung

Problemstellung.
 Definition eines analog arbeitenden Perzeptors.
 Realisierung.
 Verfahren der Extremwertbestimmung.
 Berücksichtigung negativer Merkmale.
 Die Lernphase.
 Weitergehende Möglichkeiten.
 Perzeptoren und Perzeption.
 Literatur.

1. Problemstellung

In einer früheren Veröffentlichung (STEINBUCH) wurde ein Verfahren beschrieben, wie gewünschte ndungen zwischen je einem endlichen Satz von ren „Eigenschaften“ e_i und einer „Bedeutung“ b_k in matrixförmiges Schaltungssystem, die Lern- ix, eingelesen werden können. Diese Lernmatrix glicht die korrekte Zuordnung der Bedeutung zu Satz binärer Eigenschaften auch noch dann, wenn Störung dieses Eigenschaftssatzes vorliegt, solange Hammingabstand zum ursprünglichen Eigen- tssatz kleiner bleibt als der Abstand zu einem ren, einer Bedeutung zugeordneten Eigenschafts-

Dieses Verhalten der Lernmatrix macht ihre Funk- unempfindlich gegenüber nicht allzugroßen zu- en Störungen des Informationsangebots, sofern Information redundant angeboten wird. Die

Der Begriff „Bedeutung“ wird hier verwendet im Sinne durch Eigenschaften codierten, einheitlichen Gegeben- (Auf eine Diskussion des Zusammenhanges mit dem utungsbegriff der Linguistik und der Semantik wird htet.)

weitergehende Aufgabe, die Ausgabe der Lernmatrix auch invariant gegenüber *systematischen Änderungen* des Informationsangebots zu belassen, solange diese innerhalb einer vorgegebenen *Klasse* bleiben, kann unter Verwendung von (z.B. zylindrischen) Lern- matrizen gelöst werden, deren Betrieb nicht eindeutig umkehrbar ist (FRANK 1961b), aber auch durch Ver- kettung oder Schichtung von Lernmatrizen. Diese Methode der Invariantenbildung ist jedoch etwas auf- wendig.

In einer anderen Veröffentlichung (FRANK 1961a) wurde die Lernmatrix als Modell der Definition von „Perzeptoren“ zugrunde gelegt. Dabei sollte jedes System von „Beobachtungsoperatoren“, d.h. von Vorrichtungen, welche jeweils einen Objektweltzustand oder eine Klasse solcher Zustände (z.B. das Vorliegen eines Zeichens aus einer definierten Klasse) registrieren, Perzeptor genannt werden. Es wurde vorausgesetzt, daß die Menge der unterscheidbaren Zustände des beobachteten Systems (der Objektwelt) endlich und die Zustände selbst durch binäre Merkmale gekenn- zeichnet sind.

Es liegt nun einerseits nahe, den mathematischen Perzeptor-Begriff auf kontinuierliche Merkmale zu verallgemeinern, und andererseits nach einer Realisie- rung der Lernmatrix zu suchen, welche stetig ver- änderliche Eigenschaftsgrößen zu verarbeiten vermag. Im folgenden Beitrag wird ein solcher Perzeptor zuerst als Operator mathematisch definiert und hernach seine nachrichtentechnische Realisierung dargestellt, deren *Struktur* der digitalen Lernmatrix entspricht. Dabei soll es sich zunächst um eine nichtdigitale Lernmatrix in der Kann-Phase handeln. (Eine nichtdigitale Lern- matrix verwendet Eingangssignale, welche nicht digi- tal sind.) Es wird gezeigt, daß sie sowohl gegen zu- fällige Störungen unempfindlich als auch zur Bildung gewisser, vor allem affiner, Invarianten fähig ist. An- schließend wird ein Verfahren entwickelt, wie die gewünschte Art der Zuordnung in das System ein- gelernt werden kann. Abschließend wird das allgemeine Problem angeschnitten, welche Forderungen an Per- zeptoren zu stellen sind, von denen gesagt werden

kann, daß sie das leisten, was in einem verallgemeinerten Sinne „Perzeption“ genannt werden kann¹.

2. Definition eines nichtdigitalen Perzeptors

Wir sagen, ein System „lerne“, wenn es ein inneres Modell der Außenwelt dieser Außenwelt anpaßt (STEINBUCH 1959a). Ein Perzeptor der im Rahmen dieser

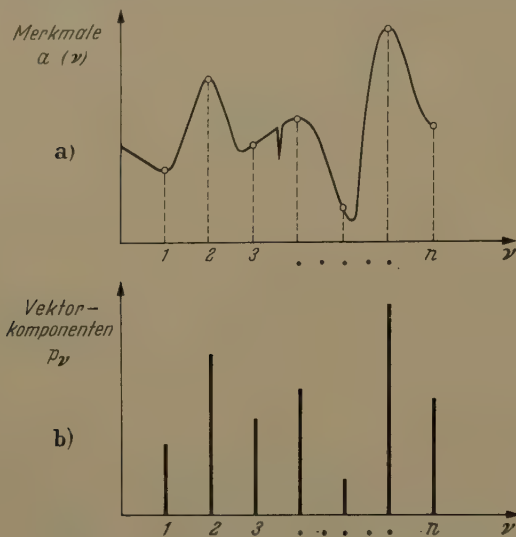


Abb. 1. Merkmalfunktion und Vektorkomponenten

Arbeit interessierenden Art muß also (als das beobachtende System) einer Außenwelt (als dem beobachteten System) gegenübergestellt werden und ein inneres veränderbares Modell dieser beobachteten Außenwelt enthalten.

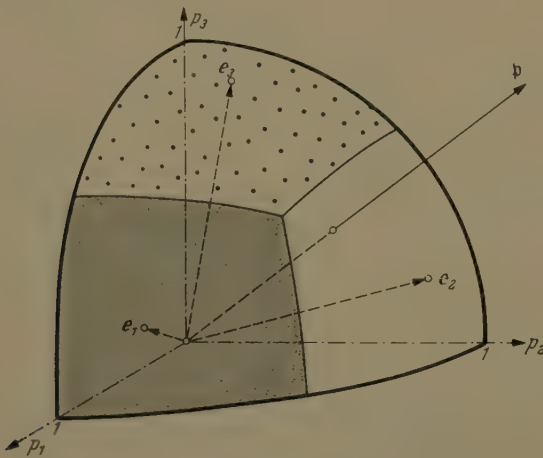


Abb. 2. Perzeptionsereignis p und Muster e_i im dreidimensionalen Vektorraum

Jedes Merkmal eines beobachteten Objekts (Außenweltzustandes) möge durch eine reelle Zahl v , $0 < v \leq n$ (n eine natürliche Zahl), gekennzeichnet werden. Beispielsweise können die beobachteten Objekte Zeitfunktionen innerhalb des Zeitintervalls $0 < t \leq n \cdot \Delta t$ sein, so daß das durch die Zahl v bezeichnete Merkmal der Funktionswert an der Stelle $t = v \cdot \Delta t$ ist. Es empfiehlt sich jedoch nicht, die Betrachtung auf diesen, wenn

¹ Diese Verallgemeinerung wurde in einer Arbeit „Über einen abstrakten Perzeptionsbegriff“ von FRANK ausführlicher dargestellt und erschien während der Drucklegung des gegenwärtigen Beitrags in Band 2, Heft 3, der „Grundlagenstudien aus Kybernetik und Geisteswissenschaft“.

auch vielleicht praktisch wichtigsten, Sonderfall, auf Zeitfunktionen, einzuschränken.

Jedes Merkmal kann verschiedenen beobachteten Objekten in verschiedenem Grade zukommen, und zwar möge es sich um eine kontinuierliche Gradschätzung handeln. Zu jedem Objekt und jedem Merkmal möge also eine reelle Zahl a_v existieren, welche angibt, daß das Objekt dieses Merkmal mit dem Grad a_v besitzt. (a_1 kann beispielsweise die Frequenz des ersten, a_2 die des mittleren und a_3 die des höchsten Tons eines Dreiklangs sein.) Das Objekt kann daher durch eine reelle Funktion $a(v)$ im Intervall $0 < v \leq n$ definiert werden (Abb. 1a).

Wir suchen nun einen Perzeptor P , der an den Punkten $v = 1, 2, \dots, n$ des Definitionsbereichs v die Funktionswerte $a_1, a_2, \dots, a_n$ von $a(v)$ ermittelt und die zwischenliegenden Funktionswerte unberücksichtigt läßt. P ist also ein Operator, der die Funktion $a(v)$ auf einen n -dimensionalen Vektor p abbildet, oder allgemein: den Objektraum aller möglichen Funktionen (dessen Koordinatenmenge die Mächtigkeit des linearen Kontinuums hat) auf den n -dimensionalen Vektorraum. Waren beispielsweise die beobachteten Objekte Zeitfunktionen, dann identifiziert alle jene Zeitfunktionen miteinander, welche an allen Abtaststellen gleiche Funktionswerte haben.

Wir denken uns P aus n Teiloperatoren zusammengesetzt, die wir Rezeptoren nennen. Der Rezeptor Nummer v ermittelt den Funktionswert a_v der Funktion $a(v)$ an der Stelle v , liefert also die v -te Partialinformation p_v über die Abbildung des Objekts a auf einen Vektor, d.h. die v -te Komponente dieses Vektors. Die Ausgabewerte $p_1, \dots, p_n$ der Rezeptoren bilden ihrerseits einen Vektor p , welcher proportional verschlüsselnden Rezeptoren mit dem Vektor $(a_1, \dots, a_n)$ numerisch übereinstimmen kann, jedoch sind auch nichtlineare Abbildungen des Objektraums auf den n -dimensionalen Vektorraum denkbar. Jede Abbildung eines durch eine Merkmalfunktion $a(v)$ gekennzeichneten Objekts auf einen Vektor p , d.h. jede Registrierung der n Funktionswerte von $a(v)$ durch die Rezeptoren von P , nennen wir ein Perzeptionsereignis p . Das Perzeptionsereignis ist definiert durch die n Ausgabewerte der Rezeptoren (Abb. 1b).

Im Falle einer Abtastung an nur $n = 3$ Stellen und positiven Merkmalfunktionen $a(v)$ kann man sich den Raum der möglichen Perzeptionsereignisse p , vorstellen als ersten Oktanten des dreidimensionalen kartesischen Koordinatensystems von Abb. 2. Wir fordern nun, daß der Perzeptor

1. alle Perzeptionsereignisse miteinander identifiziert (d.h. zum selben Ausgabewert verarbeitet), welche sich nur im Betrag $|p|$ nicht aber im Winkel zu den Koordinatenachsen des n -dimensionalen Vektorraums unterscheiden und

2. unempfindlich gegen geringe Schwankungen dieses Winkels ist.

Dies läuft darauf hinaus, den Oktanten in Abb. 2 in Sektoren unterzuteilen, so daß alle im selben Sektor liegenden Vektoren miteinander identifiziert werden. Die Sektoren bestimmen also Klassen b_i von Vektoren. Dabei sieht man jedoch, daß die Grenzen zwischen diesen Sektoren, z.B. in einer vorausgehenden Lernphase, festgelegt sein müssen, bevor ein Perzeptionsereignis zu einem Ausgabewert verarbeitet wird.

n. Das heißt, die Klassen müssen definiert sein, oder die Vektoren in sie eingeordnet werden können. Diese vorzugebenden Klassen sind nun gerade das „innere Modell“ der Außenwelt, das im Perzeptor P gespeichert sein muß. Genauer: in P muß ein (endliches) Repertoire der zu erwartenden Perzeptionsereignisse vorhanden sein, so daß jedes eintretende Perzeptionsereignis als Realisierung des nächstähnlichen erwarteten Perzeptionsereignisses gewertet wird. Die erwarteten Perzeptionsereignisse können der mathematischen Einfachheit halber m verschiedene Einheitsvektoren e_i sein, denen in der Außenwelt die „Muster“ entsprechen. Die erwarteten Perzeptionsereignisse bestimmen sogenannte „Perzeptionsformen“, in welche jede aufkommene Information eingeordnet wird, „einrastet“. Diese erwarteten Perzeptionsereignisse $e_1, e_2, \dots, e_m$ sind genauer gesagt gespeichert als Perzeptionsformen g_i , die logisch saubere Trennung zwischen abgetasteten Merkmalen $a_1, \dots, a_n$, dadurch gewonnenen Partialinformationen $p_1, \dots, p_n$ als Verschlüsselungen dieser Merkmale und zugleich als Komponenten des Perzeptionsereignisses p , und schließlich den Komponenten $\dots, g_{i_n}$ der Perzeptionsform g_i als des inneren gespeicherten Modells gewisser, durch die Muster bekannter, Perzeptionsereignisse einheitlicher Größe e_i , entspricht, da alle diese Größen auch in der Realisierung zu unterscheiden sind. Nur in Spezialfällen, in denen nämlich die einzelnen Abbildungsvorgänge proportionale Verschlüsselungen darstellen, besteht numerisch kein wesentlicher Unterschied zwischen den p und den p_v bzw. zwischen den e_i und den g_i .

Die Forderung (1) ist nun dadurch zu erfüllen, daß jedes Perzeptionsereignis der Form $p = c \cdot e_i$ unabhängig von dem positiven Faktor c (der Länge des Vektors p) zur selben Ausgabe führt. Der Forderung (2) können wir dadurch nachkommen, daß ein Perzeptionsereignis p mit demjenigen erwarteten Ereignis e_i identifiziert wird, mit dem es das größte innere Vektorprodukt $p \cdot e_i$ bildet. (Im Perzeptor selbst liegt e_i natürlich nur in der gespeicherten Form g_i vor, so daß tatsächlich das Vektorprodukt $p \cdot g_i$ gebildet wird.) Durch die e_i werden damit die gewünschten Sektoren des Raumes der p erzeugt, deren Schnittlinien mit der Einheitskugel in Abb. 2 eingezeichnet sind. Man kann diesem dreidimensionalen Falle also sehen, daß z. B. ein eingezeichnete Vektor p in die durch e_2 gebildete Klasse fällt. Man kann also die bisherigen Überlegungen zusammenfassend so beschreiben:

Das innere Modell von P besteht aus m Perzeptionsformen g_i , welche Klassen möglicher Perzeptionsereignisse p bilden. Die p selbst sind Verschlüsselungen der durch die Merkmale $a(v)$ bestimmten, beobachteten Zustände bzw. Objekte der Außenwelt durch die Perzeptoren von P . In jede Klasse b_i fällt genau eines der erwarteten Perzeptionsereignisse e_i . Dabei gehört zur Klasse b_x , falls für alle i gilt $p \cdot e_i \leq p \cdot e_x$ (und damit auch $p \cdot g_i \leq p \cdot g_x$).

Die inneren Produkte $I_i = p \cdot g_i$ sind noch vom Betrag des Perzeptionsereignisses abhängig, jedoch werden alle I_i mit derselben positiven Zahl c multipliziert, sobald p mit diesem Faktor multipliziert wird, d. h. aber, daß der Index, welcher das maximale innere Produkt kennzeichnet, derselbe bleibt — obwohl sich mit dem Betrag von p auch die Größe des Maximums ändert. Die Organe des Perzeptors P müssen daher zusammenfassend sein

1. Rezeptoren, welche die Merkmalfunktion $a(v)$ an n Stellen v abtasten und durch die Komponenten p_v von p verschlüsseln.

2. m Vektoren g_i , welche als gespeicherte Perzeptionsformen dem Repertoire der erwarteten Perzeptionsereignisse e_i einheitlichen Betrags entsprechen und damit das innere Modell der Außenwelt ausmachen.

3. Eine Vorrichtung, welche für jedes Perzeptionsereignis die inneren Produkte $I_i = p \cdot g_i$ mit der gespeicherten Form g_i bildet.

4. Eine Vorrichtung, welche bestimmt, zu welchem Index i das maximale innere Produkt I_i gehört (Extremwertbestimmung) und demgemäß als Ausgabeinformation des Perzeptors mitteilt, daß das beobachtete Objekt in die entsprechende Klasse b_i fällt.

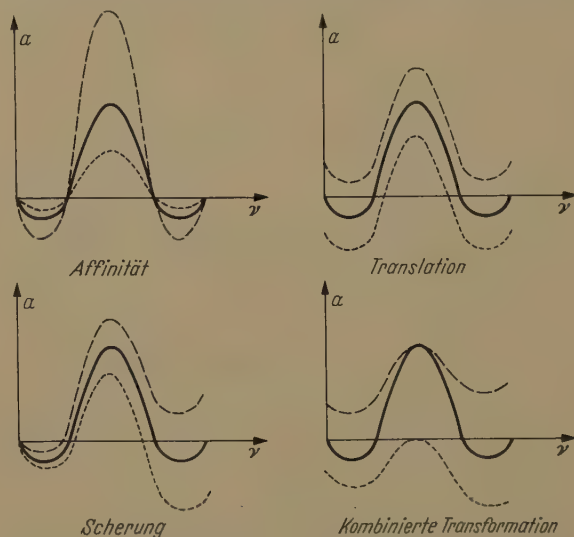


Abb. 3. Mögliche Invariantenbildungen

(Die Ausgabe kann also als System von m binären Beobachtungsoperatoren b_i aufgefaßt werden, von denen jeder mitteilt, ob das Objekt in die von ihm beobachtete Klasse fällt oder nicht.)

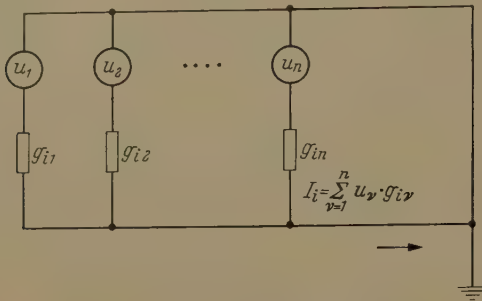
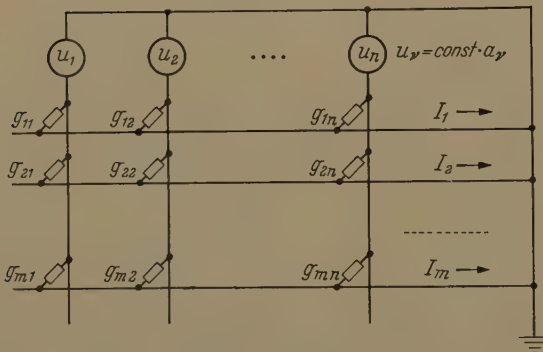
Überlegt man schließlich, was in Abb. 1 b geändert werden kann, ohne daß ein anderer Beobachtungsoperator von P anspricht, dann ist es

1. die Multiplikation aller Ordinatenwerte p_v mit derselben positiven Zahl c , also eine affine Transformation der p_v ;

2. die Überlagerung einer Störung nicht zu großer Effektivwerte, die also im Mittel die Verhältnisse zwischen den einzelnen Ordinatenwerten (d. h. in Abb. 2 den Winkel von p mit den Koordinatenachsen) nicht zu stark verändert.

Man beachte, daß der Perzeptor P genau dann eine (störungsunempfindliche) Invariantenbildung gegenüber affinen Transformationen von $a(v)$ mit der v -Achse als Affinitätsachse leistet, wenn die Verschlüsselungen p_v der a_v durch die Rezeptoren proportional zu den a_v sind. Andere Verschlüsselungen gestatten andere Invariantenbildungen. Beispielsweise kann p_v proportional zur 1. Ableitung $a'(v)$ bzw. zum ersten Differenzenquotienten, also zu $a_v - a_{v-1}$ sein; dann ist die Aussage des Perzeptors invariant gegen Translationen der Merkmalfunktion in Ordinatenrichtung und zugleich gegen affine Transformationen. Bei proportionaler Verschlüsselung der 2. Ableitung $a''(v)$ ergibt sich zusätzlich Scherungsinvarianz, usw. (vgl. Abb. 3). Natürlich müssen dabei auch die gespeicher-

ten Perzeptionsformen g_i dem Differential- oder Differenzenquotienten der Merkmalfunktion entsprechen. Andere Invariantenbildungen ergeben sich durch geeignete nicht-linear arbeitende Perzeptoren, d.h. mathematisch durch geeignet zu wählende Funktionen $p_v = f(a_v)$.

Abb. 4. Darstellung des inneren Produkts $p \cdot g$ Abb. 5. Darstellung des Produkts $G \cdot p' = b$

3. Realisierung

Der Perzeptor P als System von m Beobachtungsoperatoren b_i kann leicht durch ein nachrichtentechnisches Modell realisiert werden, z.B. wenn dafür gesorgt wird, daß die vorzuschaltenden Abtastrecep-



Abb. 6. Photographie des Modells der nichtdigitalen Lernmatrix

toren die a_v durch Spannungswerte u_v verschlüsseln, daß also $p_v = u_v$ ist. Das innere Produkt $I_i = u \cdot g_i$ wird dann durch Leitwerte g_{iv} gemäß der Schaltung in Abb. 4 realisiert. Um gleichzeitig alle inneren Produkte I_i zu erhalten, genügt es, m solche Zeilen parallel zu schalten (Abb. 5). Eine abschließende Schaltung (vgl. den folgenden Abschnitt) ermittelt die Zeile mit dem größten inneren Produkt (d.h. also der größten Stromstärke) I_i und bewirkt demgemäß eine Anzeige

am Ausgang b_i bei gleichzeitiger Sperrung aller anderen Ausgänge.

Eine Demonstrationsmodell der hier beschriebenen Art ($n=5$ Eingangswerte, $m=5$ Beobachtungsoperatoren) zeigt Abb. 6.

Als Anwendungsbeispiel erwähnten wir eingang die Erkennung von Zeitfunktionen. Soll eine Zeitfunktion $s(t)$ durch die Receptoren des beschriebenen Perzeptors abgetastet und verschlüsselt werden, dann muß sie zunächst in eine Raumfunktion $a(v)$ umgewandelt werden. Dies ist durch eine reflexionsfrei abgeschlossene Laufzeitkette der in Abb. 7 angedeuteten Art möglich. Die umgekehrte Aufgabe, Raumfunktionen durch eine derartige Kette in Zeitfunktionen zu verwandeln ist ebenfalls unter Verwendung von Laufzeitketten möglich, interessiert im Rahmen vorliegender Untersuchung jedoch nicht.

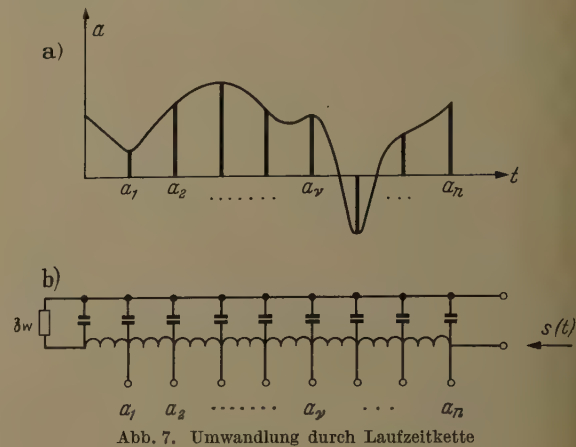


Abb. 7. Umwandlung durch Laufzeitkette

4. Verfahren der Extremwertbestimmung

Als wesentliches Bauelement bei der nachrichtentechnischen Realisierung des zunächst nur abstrakt mathematisch beschriebenen Perzeptors erwies sich eine Schaltung zur Extremwertbestimmung erforderlich, wie sie auch bei der früher beschriebenen, digital arbeitenden Lernmatrix benötigt und dort anhand einer einfachen Realisierung beschrieben wurde (STEINBUCH 1961).

Praktisch wird man jedoch nicht mit der dort angegebenen Relaischaltung arbeiten, sondern mit elektronischen Schaltelementen, wie Abb. 8 entnommen werden kann.

Abb. 8 zeigt drei Möglichkeiten zur Extremwertbestimmung. In allen drei Fällen wird die Aufgabe gelöst, denjenigen Zweig zu bestimmen, an welcher die angelegte Spannung u_i (die ein Maß für die Erregung I_i ist), den größten Wert hat. Als Maximum Indicator kann man sich beispielsweise ein elektromagnetisches Relais vorstellen, welches bei einem gewissen Mindeststrom für den zugehörigen Zweig anspricht, und dabei die Aussage liefert, daß an diesem Zweig maximale Erregung I_i auftrat.

5. Berücksichtigung negativer Merkmale

Die Merkmalfunktion $a(v)$ war in Abb. 1a überall positiv gezeichnet worden, obgleich wir bei der mathematischen Gedankenführung in § 2 von dieser Eigenschaft nirgends Gebrauch machten. Auch bei der Realisierung in § 3 war diese Einschränkung unwesentlich, da zur proportionalen Verschlüsselung

Damit ist der oben allgemein definierte Perzeptor gleicher Allgemeinheit realisiert durch eine Matrixstruktur, welche sich als Generalisierung der in der letzten früheren Arbeit beschriebenen Lernmatrix darstellt. Eine Schaltung gleicher Struktur aber mit nicht notwendig digitalen Eingangssignalen erweist, wobei allerdings zunächst nur die Kann-Phase berücksichtigt

6. Die Lernphase

Es entsteht nun die Aufgabe, die Komponenten g_{iv} eingespeicherten Perzeptionsformen (welche das Repertoire der erwarteten Perzeptionsereignisse ausmachen) nicht fest vorzugeben, sondern in einer vorausgehenden Lernphase dadurch in das System einzufügen, daß den Rezeptoren gewisse $a(v)$ als Muster gegeben und zugleich ein Signal auf jeweils den gleichen Ausgang b_i gegeben wird, der in der Kannphase Identifikation des erneut vorgelegten Musters bzw. des zur selben Klasse gehörigen Objekts mit dem eingespeicherten Bild des Musters anzeigen soll. Dabei werden die g_{iv} zweckmäßigerweise nicht durch Leitungen, sondern durch elektromagnetische Größen realisiert.

Das hier vorgeschlagene Verfahren besteht darin, die Größen $g_{i\nu}$ einer beliebigen *eingespeicherten* Rezeptionsform festgestellt und mit den betreffenden Komponenten der in eben diese Zeile *einzulernen-* Perzeptionsform verglichen werden. Aus der Differenz beider Beträge wird eine Größe abgeleitet, die die $g_{i\nu}$ nur dieser Zeile derart beeinflusst, daß die Differenz beider Beträge kleiner wird und sich schließlich dem Wert Null nähert.

Dieses Verhalten ist mit dem eines Regelkreises gleichbar. Die Größe des angebotenen, also ein-
 renden Merkmals entspricht dem Sollwert, die
 Größe des q_{iv} dem Istwert, und die Differenz beider

der Regelgröße. Hieraus wird eine Stellgröße abgeleitet, welche g_{iv} so verändert, daß die Regelgröße ein Minimum und im Idealfall Null, g_{iv} also proportional dem einzulernenden e_{iv} wird.

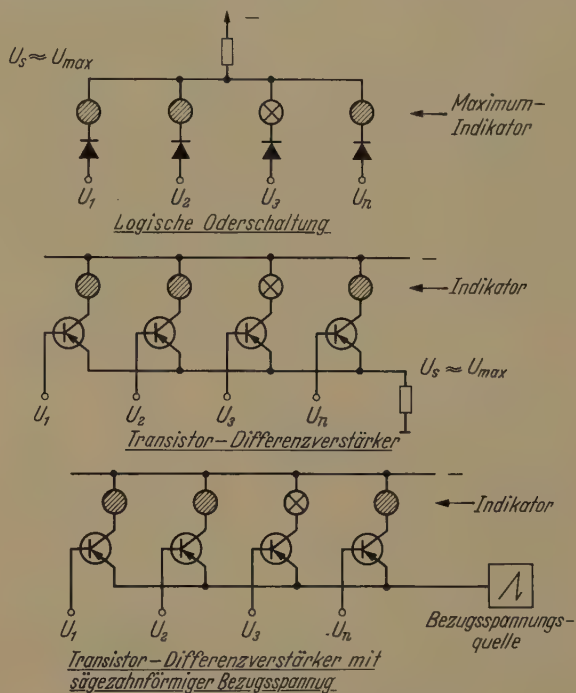


Abb. 8. Schaltungen zur Extrembestimmung

Das Verfahren sei an Hand von Abb. 10 erläutert. Als Komponenten g_i , werden ferromagnetische Anordnungen, z.B. Ferritkerne oder Bandkerne verwendet.

Die Komponente $e_{i,v}$ der zu lernenden Perzeptionsform werden durch Gleichspannungen $a_{i,v}$ repräsen-

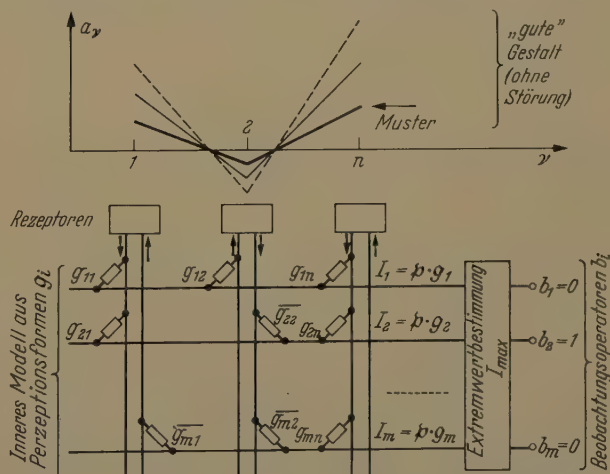


Abb. 9. Invarianz gegenüber affinen Transformationen

tiert. Dies entspricht der Sollwerteingabe bei einem Regelkreis. Durch Schließen des Schalters B_i wird der Lernprozeß einer Perzeptionsform in die i -te Zeile vorbereitet, unter Mitwirkung des Lese- und Schreibgenerators. Nach Schließen des Schalters B_i fließt in der i -ten Zeile ein hochfrequenter Wechselstrom, dessen Amplitude und dessen Frequenz so zu wählen sind, daß der Induktionszustand der Ringkerne nicht geändert wird. Der hochfrequente Wechselstrom induziert in den Spaltendrähten 2 eine Wechselspannung U , die infolge der nichtlinearen Kennlinie

der Ringkerne einen Spannungsanteil der doppelten Frequenz des erregenden Wechselstromes enthält (2. Oberwelle). Die Amplituden und die Phasen dieser Oberwellenspannungen hängen vom magnetischen Zustand der Ringkerne ab, der zunächst beliebig sei. In den Leseverstärkern L.V. werden die Oberwellenspannungen phasenrichtig demoduliert und in zu ihnen proportionale Gleichspannungen a'_{iv} umgeformt, die als Istwert ebenso wie die Sollwerte a_{iv} einer Vergleichsschaltung V.S. zugeführt werden. In dieser wird der Istwert a'_{iv} mit dem Sollwert a_{iv} verglichen und ein Differenzstrom S_0 abgeleitet, der aus einem Anteil S_{iv} , hervorgerufen durch die dem Merkmal a_{iv} zugeordnete Spannung, und einem Anteil S_{iv}' , erzeugt durch die (aus der vom magnetischen Zustand

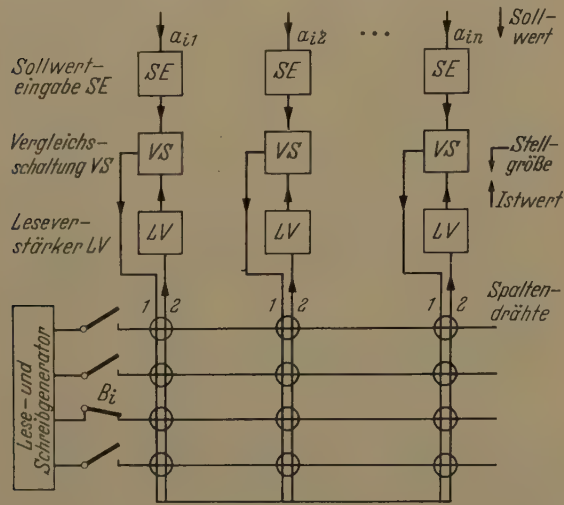


Abb. 10. Lernphase

des Ringkerns abhängigen Oberwellenspannung abgeleitete) Spannung a'_{iv} besteht, und der Differenz beider Spannungen proportional ist:

$$S_0 = S_{iv} - S_{iv}' = \text{const} \times (a_{iv} - a'_{iv})$$

S_m sei der Strom, der den magnetischen Zustand eines Ringkerns gerade zu ändern vermag. Dann ist zu fordern, daß

$$S_0 < S_m$$

bleibt, damit in sämtlichen übrigen Ringkernen der betreffenden Spalte, die nicht der ausgewählten i -ten Zeile zugehören, der Induktionszustand unverändert bleibt.

Ebenso bestand auch die Forderung, daß die Amplitude des hochfrequenten Wechselstromes so klein ist, daß der Wechselstrom allein den Induktionszustand des Ringkerns nicht beeinflussen kann. Erst durch das Zusammenwirken des Differenzstromes und des Hochfrequenzstromes, wird in den Ringkernen längs der durch Schließen des Schalters B_i ausgewählten Zeile der Induktionszustand verändert, und zwar so, daß die Abweichung der dem magnetischen Zustand der Kerne entsprechenden Gleichspannungen a'_{iv} von den, den einzulernenden Merkmalen adäquaten Gleichspannungen a_{iv} , verringert wird und sich dem Werte Null nähert. Wird die Abweichung Null, so wird auch der Differenzstrom S_0 zu Null, und zufolge der vorher geforderten Bedingung für die Amplitude des Wechselstromes kann keine weitere Beeinflussung des Induktionszustandes der Ringkerne eintreten. Dies bedeutet aber: Werden in einer nachfolgenden

Kannphase die Ringkerne der i -ten Zeile abgefragt, so induziert jeder Ringkern in einer Abfragewicklung, welche in der Kannphase durch den Zeilendraht dargestellt ist, eine Ausgangsspannung, deren 2. Oberwellen nach phasenrichtiger Demodulation und Gleichrichtung gerade derjenigen Gleichspannung entspricht, welche die betreffende Komponente der zuvor gelernten Perzeptionsform repräsentiert. — Die technische Realisierbarkeit dieses Verfahrens, das einen ersten Entwurf darstellt, wird z. Z. an unserem Institut untersucht.

7. Weitere Möglichkeiten

Die Merkmalfunktion $a(v)$ ist als eindeutige Funktion vorausgesetzt worden. Bei flüchtiger Betrachtung des in § 2 Gesagten könnte dies als starke Einschränkung empfunden werden. Denn affine Transformationen werden in der Geometrie vor allem auch auf mehrdeutige Funktionen, wie Ellipsen, Hyperbeln, Trapeze usw. angewandt. An dieser Stelle zeigt sich nun der Vorteil der oben versuchten, möglichst sorgfältigen begrifflichen Unterscheidung. $a(v)$ sollte kein als Objekt betrachtete Funktion sondern eine Funktion sein, welche angibt, in welchem Grade das willkürlich durch die reelle Zahl v gekennzeichnete Merkmal einem betrachteten Objekt zukommt. Nur in Spezialfällen, z. B. wenn Zeitfunktionen als Objekte fungieren, fällt $a(v)$ praktisch mit dem beobachteten Objekt zusammen.

Jede praktisch vorkommende Figur (Ellipsen, Schriftzeichen usw.) läßt sich als endlich-vieldeutige Funktion auffassen, und jede endlich-vieldeutige Funktion läßt sich in eine endliche Anzahl von Zweigen zerlegen, die ihrerseits eindeutige Funktionen sind und durch eine Merkmalfunktion $a(v)$ beschrieben werden können. Die Zahl der Merkmale wird aber durch die dadurch erforderliche Multiplikation mit einer natürlichen Zahl nicht geändert. Man könnte beispielsweise die z Zweige als Fortsetzungen des ersten Zweigs definieren und damit den Definitionsbereich von $0 < v \leq n$ auf $0 < v \leq zn$ erweitern (Abb. 11 b) und hier nach die reellen Zahlen v , welche je ein Merkmal bezeichnen, durch die reellen Zahlen v/z ersetzen (Abb. 11 c). Der Definitionsbereich aller z Zweige wird einheitlich von 0 bis n angesetzt, d. h. etwa vorhandene Kurvenstücke, in denen zwei Zweige übereinstimmen, erscheinen doppelt (vgl. Abb. 11 a und 11 b). Natürlich ist auch jede beliebige Vertauschung in der Ordnung der Merkmale möglich. Das Wesentliche ist, daß für alle Zweige derselbe Affinitätsfaktor c relevant ist, wie es ja bei der affinen Abbildung einer Figur im Sinne der Geometrie der Fall ist. Die Abtastung einer solchen Figur kann (Zusammengesetztheit aus nur zwei Zweigen vorausgesetzt) beispielsweise dadurch erfolgen, daß an allen Stellen $x = 2v$ des zweidimensionalen Objekts der kleinste und der größte Abszissenabstand der Figur ermittelt wird (Abb. 11 a), wobei dieser das Merkmal $a(n/2 + v)$, jener das Merkmal $a(v)$ liefert (Abb. 11 c).

Durch dieses Prinzip ist auch das in § 2 erwähnte Problem der Erkennung eines Akkords als einer dreideutigen, konstanten Funktion der Zeit lösbar (und allgemeiner: die Identifikation eines mehrstimmigen musikalischen Themas, das gegenüber dem eingelernten Muster in eine andere Tonart transponiert wurde, d. h. dessen Frequenzen alle mit demselben Faktor

multipliziert sind). Als Ordinatenwerte fungieren hier Frequenzen, als Abszissenwerte die Zeit, so daß in derselben Weise wie in Abb. 11 eine endlich-vieldeutige Funktion durch eine geeignete Verknüpfung der Receptoren in eine eindeutige Funktion transformiert wird.

Da die Extremwertbestimmung die Information über den Effektivwert c des Perzeptionsereignisses $c = c_i$ unterdrückt, ist ihre Funktion nicht eindeutig umkehrbar. Der Umkehrbetrieb führt, falls die Funktion der Receptoren eindeutig umkehrbar ist, zur Erstellung der *Muster*, deren inneres Modell die gespeicherten Perzeptionsformen sind.

Die in den Erregungshöhen I_i der Beobachtungsoperatoren b_i liegende, durch die Extremwertbestimmung unterdrückte Information ist aber mit erheblicher Redundanz behaftet, falls die vorgesehenen Muster, d.h. die „Perzeptionsformen“ bekannt sind.

Fälle der binären Lernmatrix in der Kannphase wurde dies näher untersucht und wird demnächst in einer Publikation von ZENDEH dargestellt. Habe eine solche „Bedeutungsmatrix“ $m = 2^n$ Beobachtungsoperatoren, dann existieren für jedes I_i $n + 1$ mögliche Stromstärken von 0 bis n . Von den $(n + 1)^{(2^n)}$ verschiedenen Kombinationen von I_i sind aber nur eine geringe Zahl möglich. Denn wenn bekannt ist, daß b_i anspricht, dann ist bekannt, daß I_i die Stromstärke n hat. Außerdem sind alle p_i und damit alle anderen Stromstärken bekannt. Tatsächlich kommen es nur 2^n verschiedene Vektoren $\mathfrak{Z} = (I_1, \dots, I_m)$ von $n(n + 1)^{(2^n)}$ möglichen vor, daher die Redundanz des Vektors $\mathfrak{Z}$.

Es ist darum möglich, das Perzeptionsereignis schon dann zu identifizieren, wenn der zugehörige Beobachtungsoperator (und sogar zusätzlich noch andere), ausfällt, aber die Stromstärken der restlichen Beobachtungsoperatoren bekannt sind. Wie diese Identifikation durch eine Matrixschaltung geleistet werden kann, wird in der Veröffentlichung von ZENDEH behandelt werden. Man sieht durch Verallgemeinerung der eben skizzierten Betrachtungen, daß solche „selbstkorrigierenden Schaltungen“, also Matrixschaltungen, die auch dann noch richtige Aussagen liefern, wenn wesentliche Teile von ihnen ausfallen oder sonstige Fehlfunktionen liefern, auch für nicht-digitale Lernmatrizen existieren müssen.

Abschließend sei noch auf die mathematische Seite des Problems hingewiesen. Die gewählte Abbildung von Abtastwerte auf einen Vektor im n -dimensionalen Raum entspricht dem Vorgehen von SHANNON (1949), der statt mit Vektoren mit Punkten arbeitet und dabei seinen bekannten Aussagen über die Kanalkapazität in der Anwesenheit von weißem Rauschen kommt. Es geht nahe, von diesen Gedankengängen ausgehend eine quantitative Theorie der Speicherkapazität der nichtbinären Lernmatrix und eine die Kannphase betreffende Theorie des maximalen Verknüpfungseffektes als nicht-digitale Verallgemeinerung des in der früheren Arbeit (STEINBUCH 1959b) Gesagten zu entwickeln. Untersuchungen darüber sind noch im Gange.

8. Perzeptoren und Perzeption

Der hier von einer früheren Arbeit (FRANK 1961a) übernommene Begriff des Perzeptors mag überraschen, er auf die Biologie oder Psychologie zu verweisen

scheint. Es gehört aber zum Wesen der Kybernetik, gewisse Begriffe einzelner Wissenschaften von unwesentlichen, nur diese Wissenschaft selbst interessierenden Bestimmungsstücken zu lösen, und sie dadurch so zu verallgemeinern, daß ihre Relevanz für eine ganze

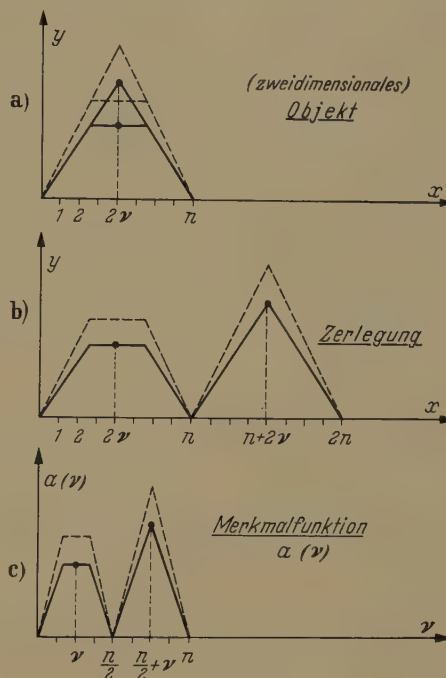


Abb. 11. Erzeugung von $a(v)$

Klasse von Wissenschaften deutlich wird. In diesem Sinne versteht A. A. MOLES (1960) unter Organismen nicht allein das, was der Biologe darunter versteht, sondern jedes genügend komplexe, auch technische oder gesellschaftliche System, das mehrere Freiheits-

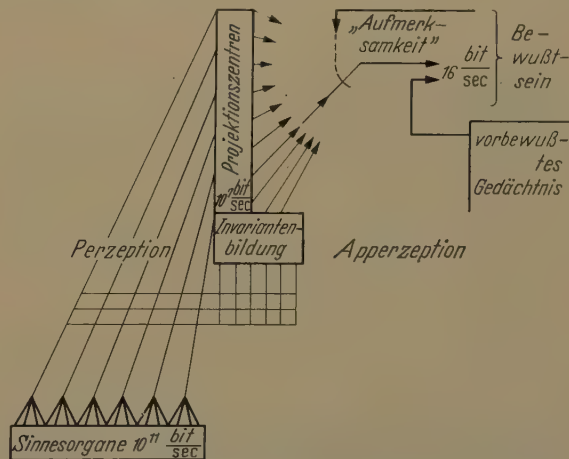


Abb. 12. Die beiden Phasen des Wahrnehmungsprozesses (schematisch)

grade der Funktion aufweist, und er definiert dementsprechend Kybernetik als die Wissenschaft von den Organismen ohne Rücksicht auf die Besonderheiten der diese konstituierenden Organe.

Man kann sich fragen, ob nicht auch der Begriff der Perzeption, der als erste Phase des Wahrnehmungsprozesses der anschließenden Phase der (bewußten) Apperzeption gegenübergestellt wird (FRANK 1961b) von unwesentlichen Besonderheiten, z.B. dem Vorhandensein einer Netzhaut oder der Basalmembran samt Haarzellen, gelöst werden kann, und welches die

verbleibenden wesentlichen Bestimmungsstücke dieses Begriffes sind.

Fünf Sachverhalte scheinen dabei wesentlich und zur Definition eines allgemeinen, abstrakten Perzeptionsbegriffes ausreichend zu sein (Abb. 12):

1. Die perzipierten Außenweltobjekte können mehr Merkmale haben, als durch die Rezeptoren registriert werden können (für den Menschen z.B. magnetische Eigenschaften), d.h. es wird bei der Perzeption nur ein Teil der in der Merkmalfunktion steckenden Information abgetastet.

2. Die durch die Rezeptoren verschlüsselte Information kann größer sein, als die als Ausgabe des perzipierenden Systems der anschließenden Apperzeption verfügbar gemachten Information. (Dies kann z.B. darauf beruhen, daß verschiedene Rezeptoren über dieselben Kanäle — Nervenfasern — ableiten, vgl. Abb. 12!)

3. Als Ausgabe erscheint nicht eine Fülle zusammenhangloser Einzeldaten, vielmehr die Einheit des identifizierten Objekts, z.B. durch Einordnung in fest vorgegebene oder eingelernte Perzeptionsformen (z.B. „Gesicht“ statt der beim Fernsehen nacheinander übertragenen und nebeneinander gestellten Teilmerkmale).

4. Verschiedene solcher Einheiten werden durch Invariantenbildung zu Klassen zusammengefaßt.

5. Der (psychologisch und philosophisch schwer fassende) Bewußtseinsbegriff ist für die Perzeption nicht relevant, im Gegensatz zur anschließenden Phase der Apperzeption, welche in der bewußten Zuwendung der Aufmerksamkeit zu Teilen der vermög der Perzeption verfügbaren Information und ihrer bewußten Verknüpfung mit Gedächtnisinhalten besteht.

Nennt man einen Organismus (im allgemeinen Sinne von MOLES), der einen Prozeß der Perzeption in diesem obigen Sinne leistet, einen Perzeptor, dann erhält man einen Begriff, der das deckt, was in § 2 als Perzeptor eingeführt wurde. Insbesondere vermag auch die nichtdigitale Lernmatrix die Funktion der Perzeption in diesem verallgemeinerten, kybernetischen Wortsinn zu erfüllen und darf daher zurecht als Perzeptor bezeichnet werden.

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The transfer function of a photoreceptor organ*

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With 9 figures in the Text

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Summary. The dynamic response of a simple ganglionic photoreceptor has been studied. It exemplifies the general processes of sensory reception and transmission of sensory information in the form of trains of nerve impulses. The experimental basis of the defining linear transfer function is presented. This transfer function is composed of a second order lag and a transport delay. The ventral nerve cord conduction time does not contribute to the transport delay. Nonlinear discrepancies from the linear model are evaluated and discussed.

Introduction

A full description of the function of a sensory organ or sensory element should include definition of the limits of signal transfer. This can be done if the stimulating energy is monitored, and at the same time, the nervous impulses emanating from the sensory receptor are detected and studied. It is believed that the signal which represents the input stimulus, and which is transmitted to other centers of the central nervous system, is the average frequency of these nerve impulses. By correlating the instantaneous values of the stimulus and the nerve impulse signal, it is possible to make a rigorous statement regarding the transfer characteristics of the sensory receptor. The task, then, is to find the equation (generally an integro-

differential equation) which characterizes the functional relationship between input and output [1—4].

Method

Photoreceptor. To explore the problem, we have chosen to study the photosensitive tail ganglion of *Cambarus astacus*, the common crayfish [5—8]. Behavioral and reflex studies have demonstrated a physiological role for the receptor [9, 10].

Fig 1 shows a photograph of the neuroanatomical structure. The terminal abdominal ganglion, a 2 mm diameter translucent neuropil, receives fibers from several sensory modes from the uropods [11], [12]. A small number (circa 10) of neurones transduce photic energy. Lack of optical apparatus, absence of apparent spatial arrays in its structure, and sluggishness of behavioral response, suggest that the ganglion serves to detect average levels of background illumination.

Through a window in the ventral abdominal exoskeleton, gross electrodes were applied to the ventral nerve cord. The animal was kept in a humidity and temperature controlled environment (100 per cent saturation, $19 \pm 0.5^\circ \text{C}$). Maintenance of adequate blood pressure and minimization of blood loss proved to be critical in the preparation. The crayfish was fixed by two bands of rubber to a corkboard in supine position. Chelipeds were sheathed in rubber

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Fig. 1. 6th abdominal ganglion of the crayfish, *Cambarus astacus*. The ganglion consists of a layer of primary and secondary neurones embedded in a dense neuropil. The photoreceptive cells are not distinguishable by current histologic techniques. They number on the order of ten. (Photograph courtesy of BRAITENBERG and IIDA)

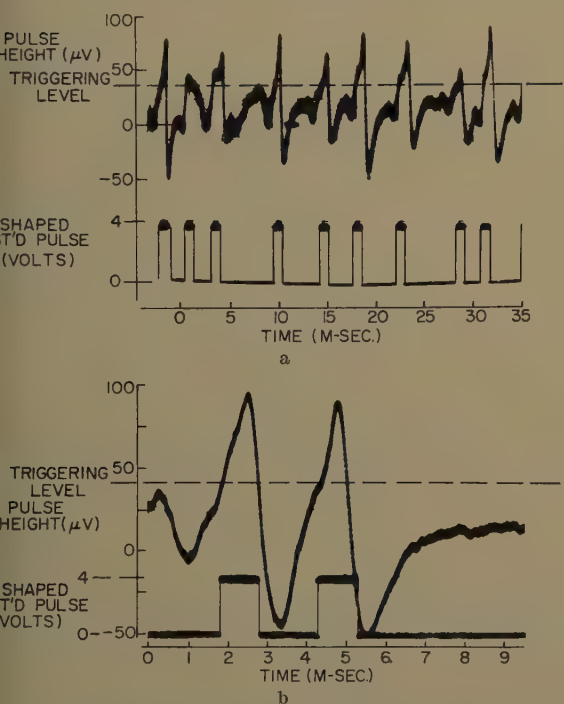


Fig. 3a and b. Pulse selection and pulse shaping. a The top trace shows the nerve-impulse train. The bottom trace shows the shaped pulses (1 msec. width) triggered at a selected level of the nerve impulse which may be either positive or negative with regard to the base line as desired. b The pulse selection and pulse shaping may be seen at greater magnification. The width of the standard pulse was set at 0.5 or 1.0 msec so as to allow for averaging but still separate trigger pulses close together in time

tubing pinned to the board. The hydrostatic level of the tail ganglion was approximated to a level several millimeters above the ventral coelom. Steady state recording of at least six hours was possible.

Apparatus. An electronically controlled light source was used to generate transient steps as well as sinusoidal variations of light. The light source contained a monitoring phototube whose output could be recorded during an experiment [13]. The light was focused to an approximately $\pi \text{ mm}^2$ spot falling on the photosensitive abdominal ganglion. The light stimulus was calibrated by means of an illuminometer. The ventral nerve cord and the other abdominal ganglia gave no response when illuminated.

Signals were led off by gross platinum electrodes to conventional A. C. amplifiers. The electrodes were hooked about the ventral abdominal cord in varying positions along the chain of ganglia. Visual monitoring of nerve impulses was not detectably altered by shifts in location of the gross platinum hook electrodes; obviously change in cross-sectional location of a given light fiber produced very little change in potential. Correlation of pulse velocity and pulse height supported the visual impression; pulses of the same height (but from different fibers) showed equal velocities wherever recorded in the cord [14]. One could also anticipate the small variation of recorded pulse height despite spatial shift of recording electrode from calculations of estimated extracellular impedance pathways [15]. The population of light sensitive neurones showed a homogeneous pulse height (and, of course, velocity) distribution.

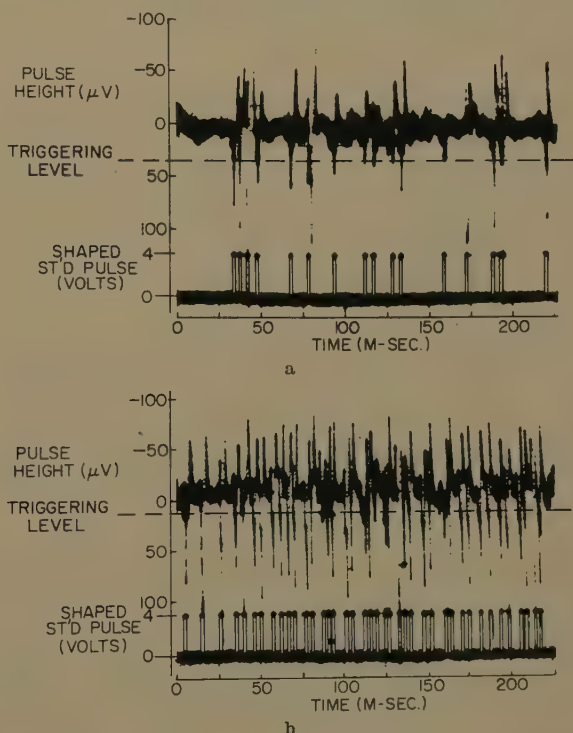


Fig. 3a and b. Nerve impulse response to light. a An example of the pulse rate with relatively low illumination. Note the large ("A"), medium-sized ("B"), and small ("C") nerve impulses. b The pulse rate increases greatly when illumination is increased. Note that this increase is due to "B" nerve impulses alone

Advantage was taken of pulse height constancy to screen out those pulses whose heights were greater or less than the pulses carrying the light signals [16].

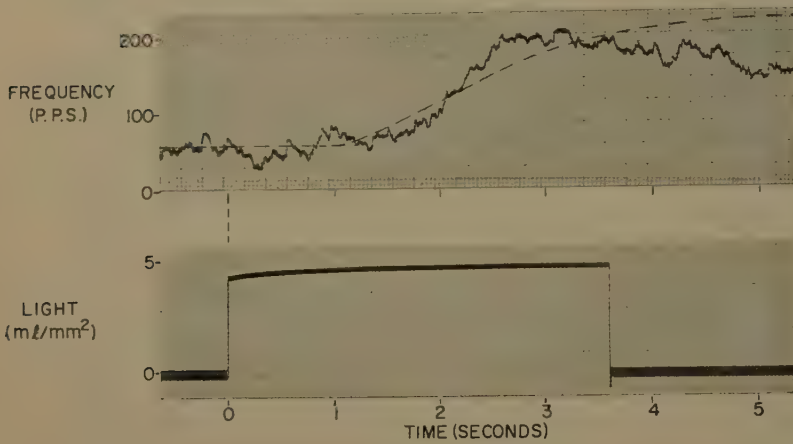


Fig. 4. Response of photosensitive ganglion to a step change of light. Shows the response of the photoganglion in terms of average frequency of nerve impulses from *B* fibers, to a step of light flux. The noise seen comes, in part from random groupings of nerve impulse from different fibers. The solid line represents the response of the linear model system described by the transfer function discussed below. The lack of fit is explained by two factors. First, random variations in a single step function are considerable. Second, the small signal approximation is violated in step experiments and certain nonlinearities produce divergences

Individual pulses whose height was greater than a preselected level triggered a standard pulse, as may be seen in Fig. 2. The pulse height groups could be

group "A" ($> 125 \mu\text{V}$) was uncorrelated. The "C" group was screened out by raising the bias level. By taking the difference of the "A" group from the remaining "A" and "B" group, a "B" window could be formed. Our results were confirmed using a conventional pulse height discrimination counter [16]. The effect of illuminating the ganglion may be seen in Fig. 3.

The standard pulses were passed through a low pass filter whose time constant (0.24 sec) was long with respect to the pulse repetition rate, but short with respect to the response frequency of the photoreceptor. The output of the low pass filter (an analog voltage whose level corresponds to the instantaneous output frequency of the neurone population) was displayed on a standard penwriter.

Experimental Section

Transient Inputs. The response of the photosensitive ganglion is measured in terms of the average frequency of firing of the population of "B" nerve fibers in the ventral nerve cord. The stimulus is recorded as the calibrated output of the monitoring photocell. A sudden change in level of illumination produces a response: rapidly increased firing rate of the nerve fiber population. Fig. 4 shows such an experiment. The response exhibits some characteristic dynamic features: long latent period, inflected rise to maximum with little overshoot or ringing, and maintenance of DC response. These features will be measured and examined in detail by means of the experiments described below. The irregularity of the baseline consists of high frequency fluctuations and low frequency drifts. Irregular grouping of the various nerve fiber impulse trains is probably the cause of much of this variation and may conveniently be treated as noise.

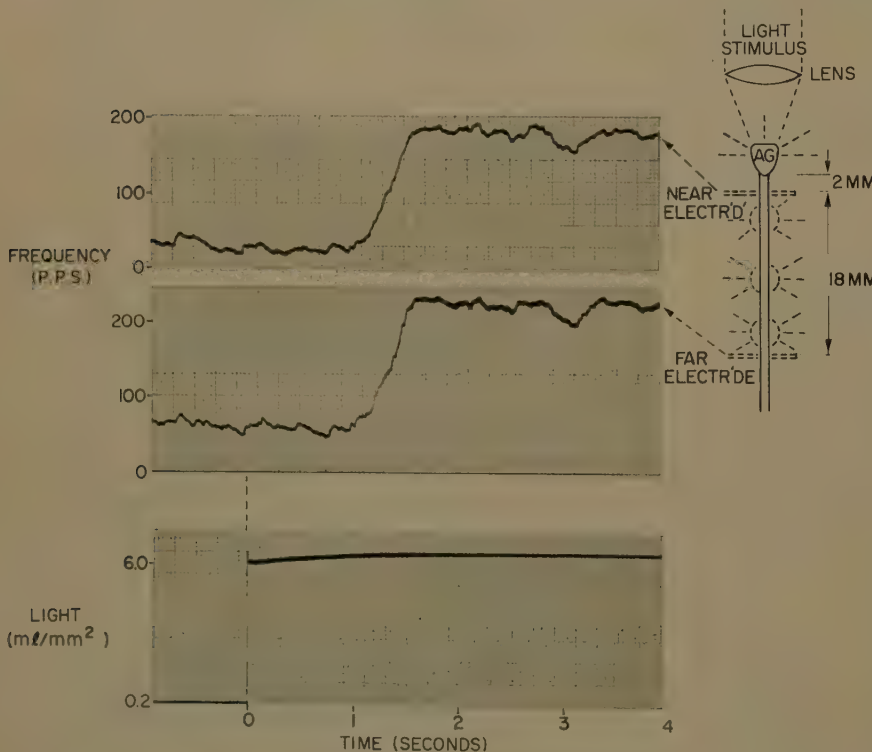


Fig. 5. Transient experiment. Fig. 5 shows the lack of contribution of nerve conduction time to the non-minimum phase element (time delay). Thus, processes in the photosensitive ganglion are responsible for this operator. Conduction velocity is approximately 4 m/sec. It is interesting to note that details of the response are preserved over the 18 mm conduction path, through three abdominal ganglia. This step of light was a rather large, violating completely the theory of small perturbation analysis. Damping is inversely proportional to forcing function amplitude

separated into three crude divisions. A midrange group "B" ($75\text{--}125 \mu\text{V}$) carried the light signal; a low voltage group "C" ($35\text{--}50 \mu\text{V}$) correlated inversely with the light fiber activity; and a high voltage

transmitted faithfully along the nerve cord, suggesting absence of synaptic relays with the attendant opportunities for convergence, divergence, and shifts in temporal patterns of the impulses.

In this experiment, rather more overshoot is apparent as the input signal was intentionally made rather large (by dark adapting the photosensitive ganglion).

Sinusoidal Inputs. In order to quantify carefully the dynamic characteristics of the photoganglion impulse response, we resorted to sinusoidal inputs. By this means we were able to subject the system to a steady state analysis. After initial conduction transients have died out, at a single frequency, the response is related to the input by two parameters only: gain (relative amplitude of input and output), phase shift (amount of lag of response after stimulus). Since such a canonical description applies only to linear systems, we attempted to approach linear operating conditions by using small stimulating signals about a steady "DC" light level¹. Further, noise and the variations in responsiveness of the ganglion were minimized by averaging responses over a number of cycles. Harmonic distortions, although present, did not contribute much power compared to the fundamental response. A set of such experiments are shown in Fig. 6.

Analysis. The dynamic behavior of the photosensitive ganglion was studied by means of frequency response experiments. This series was so devised as to eliminate trends. The driving frequencies were randomly ordered inside of each sequence and the sequences repeated. No sequence coincided in order of frequency presentation, but each sequence spanned the entire spectrum.

The gain and phase parameters averaged within each run are plotted in Fig. 7. From this Bode plot one can obtain several quantitative measures of the dynamics of the system. The low frequency gain is 32 pulses per second per millilumen. The break frequency, clearly shown by means of asymptotes drawn to fit the experimental curve, was found to be 0.2 cycles per second. Above this frequency the response attenuates with a minus two slope (12 decibels/octave, 40 db/decade or 20 decilog/decade). At the break frequency, the gain is down 6 decibels or decilog from the low frequency value. The phase curve shows a great deal of phase lag near the low frequency, high gain response region. This will be seen to be due to a large non-minimum phase element.

The phase curve represents a theoretical composite curve whose elements can be seen clearly in Fig. 8.

Here, the phase contribution of the minimum phase elements (computed from the minus two slope and the break frequency) is added to a phase lag introduced by a deduced non-minimum phase element (transport delay or latent period of 1 sec). The composite phase curve adequately fits the experimental data.

Having obtained the above quantitative measurements from the Bode Plot we may construct a transfer function, in terms of the Laplace transform complex variable " s ".

$$Y(s) = \frac{32 e^{-1.0s}}{(1 + 1.2s)^2} \text{ pulses sec}^{-1} \text{ millilumen}^{-1} \quad (1)$$

The important parameter to minimize in order to achieve linearization is the degree of modulation with respect to the level of light and not the absolute amplitude of the input sinusoidal function.

where 32 is the low frequency gain, $e^{-1.0s}$ represents the non-minimum phase element or delay time, and $(1 + 1.2s)^2$ defines the second order critically damped lagging elements which attenuate the high frequency response.

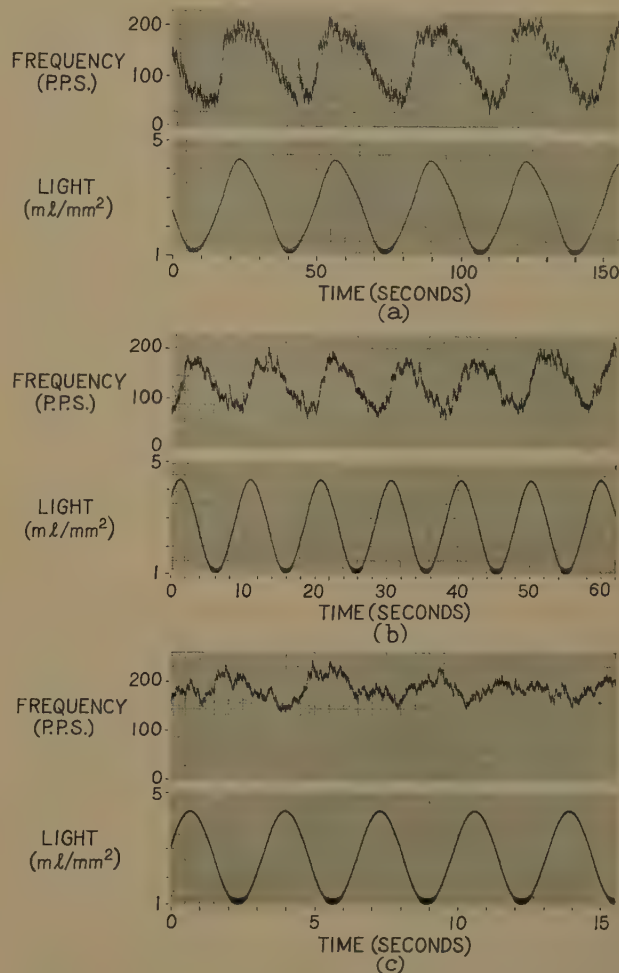


Fig. 6. Response of a photoreceptor to sinusoidal light changes. Note that harmonic distortion is minimized by small signal approach. The 0.03 cps input produces an output with amplitude of ± 70 pps, a mean of 130 pps, and a phase lag of 22° . The 0.10 cps input shows an output amplitude of ± 50 pps and a mean of 146 pps. The 0.30 cps input shows an output amplitude of ± 40 pulses per second and a mean of 154 pulse per second. The monotonic but not regular increase of the mean may be related to system nonlinearities which distort the response shape

A less convenient form is the classical integro-differential equation

$$32L(t-1) = 1.44 \frac{d^2P}{dt^2} + 2.4 \frac{dP}{dt} + P \quad (2)$$

where L = light flux in millilumens; P = pulses per seconds; t = time in seconds.

The polar plot of gain as a function of phase lag provides another graphic display of system dynamics. Frequency is a monotonically increasing, but not regularly increasing function in the clockwise direction. The non-minimum phase element, the time delay, spirals the curve about zero with a phase lag proportional to frequency. The lack of adaptation is clearly demonstrated by the absence both of phase advance and low frequency attenuation in the range studied (see Fig. 9).

Step Analyses. From the transfer function one can construct the theoretical response of the linear system to a step change of light. This computed

response is shown in Fig. 4 as the dashed line superimposed (for comparison) upon the experimentally found response. The differences are striking and outside the limits of experimental error. The com-

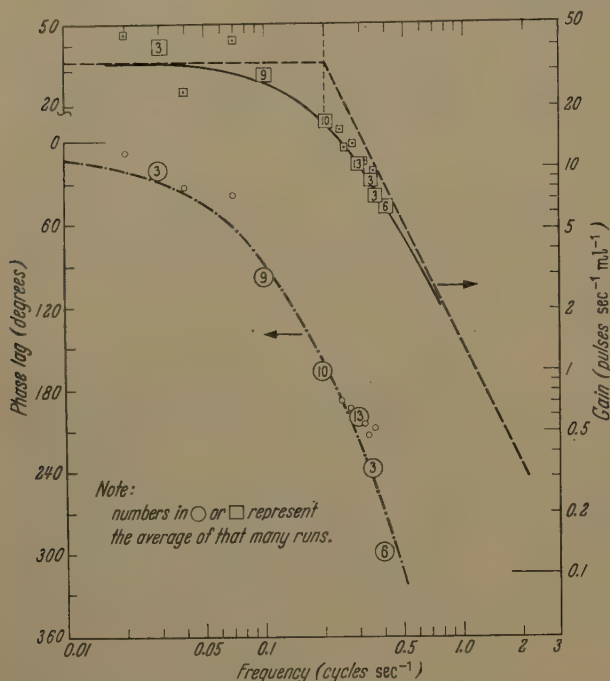


Fig. 7. Bode plot. Gain is plotted on a log-log scale, phase lag on linear-log scale. The points are experimental. The continuous line of the gain plot is guided by the asymptotes on either side of the break frequency. The response is down 6 decibels at the break frequency of 0.2 cps which is characteristic of a second order system. The phase lag curve is computed from the sum of the minimum and non-minimum phase elements (Fig. 8)

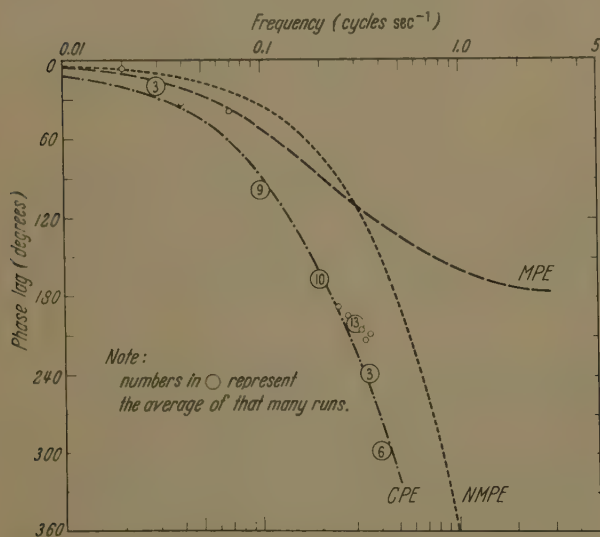


Fig. 8. Bode plot. Decomposition of phase elements. The composite curve CPE is computed from the joint contributions of the non-minimum phase elements (NMPE) and minimum phase elements (MPE). The MPE (lag elements) are computed from the experimentally obtained equation of the second order system $\frac{1}{(1 + 1.2s)^2}$. The NMPE is due to transport delay (1.0 sec) and represents the element which when added to the MPE, produces a good approximation to the experimental data. Note that no phase advance appears in the frequency range studied. The points are experimental

puted response has been obtained by linearized (small signal) approximation to the real system.

The step experiments in Figs. 4 and 5 clearly violate the small signal approach utilized in the frequency

response studies. The discrepancies are due to nonlinearities which become significant in the (large signal) step experiments. These will be reported in a following study.

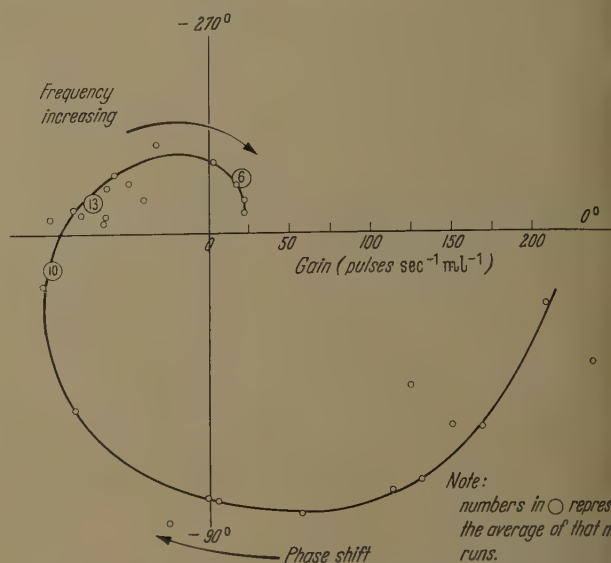


Fig. 9. Polar plot of the transfer function. Polar plot representation of gain to phase of output versus input. The solid line is computed from the actual curves of gain and phase lag in the Bode diagram (Fig. 7). Note the absence of phase advance. Frequency increases monotonically but not regularly in a clockwise direction. Phase lag increases due to a constant delay (non-minimum) element. The gain decreases as the phase lag increases at higher frequencies. Phase lag and gain combine to account for the spiral in toward zero

Discussion

Several interesting features of the crayfish photoreceptive ganglion response should be stressed. First, it is a population response; and although much of the noise (not at all germane to the biological system) is contributed, certain other experimental advantages accrue, namely, an averaging of response over short and long periods of time. PRINGLE and WILSON, working with a cockroach proprioceptor, were able to obtain only inconsistent data: steps and three frequency points [1]. The crayfish ganglion was also advantageous in having a maintained DC response and a frequency response slow with respect to the pulse repetition rate.

The slow dynamics and the long latent period suggest that the ganglion photoresponse drives a tonic reflex; and indeed this is so. The random walk response is a low priority response which shows itself only if more active behavior is called for. Then, high light level produces a photokinetic random walk into the region of subdued illumination [10].

The small signal requirement for linear approximation only partly eliminated persistent nonlinearities: asymmetrical response, DC level dependence on driving frequency, harmonic distortion. When a large signal, as in the step experiments of Figs. 4 and 5, is employed, departures from linearity can be marked. The linear response predicted from the transfer function should be symmetrical about the inflection point, and critically damped, without overshoot or ringing. In certain amplitude ranges, an inverse relationship holds between damping and input amplitude. Despite these observed deviations from linearity, the experimental analysis above has succeeded in defining t

system dynamics with considerable validity. The population averaging, the stationarity of the preparation, the fact that the frequency response range is much slower than the pulse repetition rate, and of course the biological factors involved in careful maintenance of the preparation have all contributed to the success of the approach. Perhaps the most significant part of the approach is the use of small signal sinusoidal inputs. Here the linear characteristics of the system can be extracted with minimum interference from nonlinearities. The ability to average over many cycles and tens of seconds of response increased the precision of the experimental measurements.

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Buchbesprechungen

Schlitt, Herbert: Systemtheorie für regellose Vorgänge. Statistische Verfahren für die Nachrichten- und Regelungstechnik. Berlin-Göttingen-Heidelberg: Springer 1960. XI, 344 S., 7 Abb. u. 1 Taf. Geb. DM 49.50.

Es war sicherlich keine leichte Aufgabe, das in den letzten Jahren angesammelte Material aus dem Gebiet der statistischen Verfahren in Nachrichten- und Regelungstechnik in einem nicht zu umfangreichen Buche zusammenzufassen. In der deutschsprachigen Fachliteratur fehlte schon seit Jahren ein geeignetes Werk, das sich mit der Anwendung statistischer Methoden bei der Behandlung nachrichtenübertragender und -verarbeitender Systeme befaßt. — Die beiden ersten Kapitel enthalten die Elemente der mathematischen Statistik, behandelt unter dem Gesichtspunkt der physikalischen Anwendungen. Auf dieser Basis baut sich die Bearbeitung des gesamten Stoffes auf. Der Reihe nach werden behandelt: Die linearen Systeme (Kapitel III), die zeitabhängigen regellosen Vorgänge und deren statistische Kenngrößen, die Korrelationsfunktionen und Leistungsspektren (Kapitel IV), die Zusammenhänge zwischen den Kenngrößen an Eingangs- und Ausgangssignalen bei linearen Systemen im Zeit- und Frequenzbereich (Kapitel V). Im sechsten Kapitel werden die bekanntesten linearen Filter im einzelnen besprochen. Schließlich werden 2 Verfahren zur Lösung nichtlinearer Probleme sowie die Synthese von Optimalfiltern dargestellt (Kapitel VII und VIII). — Bei der Einteilung des Stoffes behält der Verfasser die didaktischen Gesichtspunkte eines Lehrbuches im Auge. Um innere Zusammenhänge herauszuarbeiten, greift er nach Einführung neuer Be-

griffe durchweg auf vorhergehende Abschnitte zurück. So wird z.B. nach Behandlung der Korrelationsfunktionen (im Kapitel IV) ein kurzer Abschnitt den Zusammenhängen zwischen Korrelationskoeffizienten (Kapitel II) und Korrelationsfunktionen gewidmet. — Besonders hervorzuheben ist das Bemühen des Verfassers, Begriffe — die leicht zu Unklarheiten und zum Überschreiten der Anwendungsmöglichkeit führen — bis in die letzten Einzelheiten klar darzustellen, die Bedeutung an praktischen Beispielen zu erläutern und den Bereich der Anwendungsmöglichkeit abzugrenzen. Es sei an dieser Stelle der Abschnitt über den Korrelationskoeffizienten und seine Bedeutung hinsichtlich der funktionalen Abhängigkeit zweier statistischer Größen, sowie das umfangreiche Unterkapitel über die Eigenschaften des Einheitsimpulses erwähnt. — Der Stoff des Buches stellt eine Verbindung zwischen verschiedenen Forschungsrichtungen dar. Dementsprechend sucht der Verfasser seine Nomenklatur der des Schrifttums der Nachbargebiete anzupassen. — Als Leserkreis für sein Buch werden vom Verfasser „Ingenieure und Physiker, sowie Studierende aus dem Bereich der Nachrichtenverarbeitung, der Informationstheorie, der Nachrichten- und Regelungstechnik“ genannt. Beim Leser werden „solide Grundkenntnisse in der Infinitesimalrechnung, der Funktionentheorie sowie in der Elektrotechnik“ vorausgesetzt. — Vergleicht man das vorliegende Werk mit zur Zeit vorhandenen fremdsprachigen (insbesondere amerikanischen und englischen) Büchern, so darf behauptet werden, daß es durch Stoffauswahl und Aufbau zu den modernsten auf diesem Gebiet gezählt werden kann.

VARJÚ (Tübingen)

Richtlinien für die Anfertigung der Manuskripte

1. *Manuskript.* Es soll einseitig mit Schreibmaschine, mit einem mindestens 4 cm breiten Rand und ausreichendem Zeilenrand (etwa 30 Zeilen pro Seite) geschrieben sein. Soweit Teile des Manuskriptes in einem kleineren Schriftgrad (Petit) gesetzt den können, sind sie durch einen vertikalen Strich am Rande unter Beifügung des Buchstabens „p“ zu kennzeichnen. Formeln, Noten und Tabellen werden automatisch in Petit gesetzt. Tabellen sind mit Überschriften zu versehen und laufend zu nummerieren.

Jedem Beitrag soll eine Zusammenfassung beigegeben werden. Für deutsche Arbeiten sind Zusammenfassungen in englischer, für lische Arbeiten in deutscher Sprache erwünscht.

Der Umfang der Beiträge soll so knapp wie möglich gehalten werden.

2. *Literatur.* Die Literaturhinweise im laufenden Text erfolgen durch Nennung des bzw. der Autorennamen, wenn es sich um einen r zwei Autoren handelt. Bei mehr als zwei Autoren wird nur der erste genannt, gefolgt von dem Zusatz „et al.“. Werden mehr eine Arbeit desselben Autors oder derselben Autorengruppe zitiert, so ist hinter dem Namen das Erscheinungsjahr der Arbeit ugeben. Stammen mehrere Arbeiten desselben Autors aus dem gleichen Jahr, werden die Buchstaben a, b, c usw. der Jahreszahl zugefügt, z. B. MEIER (1958a).

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Zeitschriftenaufsätze werden zitiert mit Namen und Initialen aller Autoren, vollständigem Titel der Arbeit in der Originalache, Titel der Zeitschrift (in der international üblichen Abkürzung), Bandnummer (bitte unterstreichen), Seitenzahl sowie in mmern gesetzter Jahreszahl.

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Bei Übernahme von Abbildungen aus anderen Werken wird um genaue Quellenangabe gebeten.

Instructions for the Preparation of Manuscripts

1. *Form of Manuscript.* The Manuscript should be typewritten, using only one side of the paper, and should have wide margins (ca. 4 cm) and be double spaced (ca. 30 lines to the page). Those sections of the manuscript that may be printed in smaller (petit) type are to be indicated by a vertical line in the margin with the letter "P". Formulae, footnotes, tables and legends will be printed in petit. Tables should be provided with a caption and numbered consecutively.

Each manuscript should be accompanied by a summary. Papers written in German should be summarized in English and vice versa.

Papers should be as short as possible.

2. *References.* References should be cited in the text by the author's name and the year of publication. When there are more than two authors only the first is named and the words "et al." are added. If only one paper by a given author is cited the year of publication may be omitted in the text. When more than one paper with the same author and year of publication is cited the papers are differentiated by a small letter following the year, e.g. MEIER (1958a).

Papers cited should appear in the Bibliography unnumbered, in alphabetical order by Author and year of publication. For papers published in periodicals give the names and initials of all authors, the full title of the paper in the original language, the title of the periodical in the standard international abbreviation, the volume number underlined, the page numbers, and the year of publication in brackets. For Books give the names and initials of the author, the full title, the edition, the places of publication, publisher, and the year of publication.

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It is requested that illustrations taken from other publications be accompanied by full information as to their source.

HARMON, L. D., Studies with Artificial Neurons, I: Properties and Functions of an Artificial Neuron. With 21 Figures in the Text	89	Neurons, III: Mechanisms of Flicker-Fusion. With 15 Figures in the Text	10
BERGELJK, W. A. VAN, Studies with Artificial Neurons, II: Analog of the External Spiral Innervation of the Cochlea. With 10 Figures in the Text	102	STEINBUCH, K., und H. FRANK, Nichtdigitale Lernmatritzen als Perzeptoren. Mit 12 Textabbildungen	11
LEVINSON, J., and L. D. HARMON, Studies with Artificial		STARK, L., and H. T. HERMANN, The Transfer Function of a Photoreceptor Organ. With 9 Figures in the Text	12
		Buchbesprechungen	12

FACHNACHRICHTEN / NOTES AND NEWS

The *Ninth International Congress of Linguists*, under the presidency of EINAR HAUGEN, will be held in Cambridge, Massachusetts, at Harvard University and at the Massachusetts Institute of Technology, from August 27 to August 31, 1962. The Congress will have five Plenary Sessions, twelve Section Meetings, and an as yet undetermined number of Group Meetings. The topics and rapporteurs for the Plenary Sessions are: "On the Methods of Internal Reconstruction", J. KURYOWICZ; "Levels of Linguistic Analysis", E. BENVENISTE; "Structural Variation in Language," A. MARTINET; "The Logical Basis of Linguistic Theory", N. CHOMSKY; and "Linguistic Aspects of Translation" (rapporteur invited). The Section Meetings, which will consist of four contributed papers each, have tentatively been assigned the following topics: Mathematical Linguistics, Phonetics and Phonemics, Linguistic Geography, Stylistics, Morphology and Morphophonemics, Technology and Linguistics, Linguistic Change, Problems of Syntax, Methods and Materials of Language Teaching, Language Universals, Structural Semantics, and Language and Society. Contributed papers that cannot be accommodated within the Sections or refer to topics other than those planned for the Sections, will be read at special Group Meetings held each day. Persons interested in receiving the official announcement of the Congress are asked to write to the Secretariat, 9th International Congress of Linguists, Room 14N-307, M. I. T., Cambridge, Mass.